An examination of the impacts of invasive woody vegetation on grassland birds and waterfowl

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Dedication

For my co-pilot, Avalon, who patiently grew old while I was working on this.

Table of Contents

Acknowledgements i

Dedication.. ii

Table of Contents... iii

List of Tables.. v

List of Figures……... vi

Preface: ……………………………………………………...……………..………… 1

Introduction: Trees and North American grassland ecosystems……………..………… 2

Chapter 1: Tree avoidance patterns of grassland songbirds

1.1 Introduction 7

1.2 Methods 10

1.3 Results 17

1.4 Discussion 21

1.5 Tables 29

1.6 Figures... 34

Chapter 2: Impact of encroaching woody vegetation on nest success of upland nesting waterfowl

2.1 Introduction ……….. 36

2.2 Study Area 38

2.3 Methods 40

2.4 Results 46

2.5 Discussion 48

2.6 Management Implications 51

2.7 Tables 53

2.8 Figures... 55

Chapter 3: Grassland birds demonstrate delayed response to experimental tree-removal

3.1 Introduction 60
3.2 Materials and Methods.. 62
3.3 Results... 67
3.4 Discussion.. 71
3.5 Tables………….. 78
3.6 Figures.. 89

Literature Cited.. 96

List of Tables

Chapter 1

Table 1: Description of variables …………………………………….………… 29

Table 2: Model description …………………………………………………….. 30

Table 3: Model selection ……………………………………………………….. 31

Table 4: Model covariates …………………………………………………… 33

Chapter 2

Table 1: Model selection ……………………………………………………….. 53

Table 2: Woody vegetation models ………...………………………………….. 54

Chapter 3

Table 1: Summary of treatment and control sites ……………………..…….. 78

Table 2: Model description …………………………………………………….. 79

Table 3: Model comparison …………………………………………………..... 80

Table 4: Summary of species counts and species group composition …………. 82

Table 5: Model coefficients ……………………………………………………. 88

List of Figures

Chapter 1

Figure 1: Model predictions for all habitat covariates …………………………………. 34

Figure 2: Response to increasing grass versus increasing woody vegetation ………….. 35

Chapter 2

Figure 1: Waterfowl nest success for multi-year study sites…………………………… 55

Figure 2: Daily nest survival……………………………………………………………. 56

Figure 3: Nest success relative to percent grass and wetland…………………...……. 57

Figure 4: Nest success relative to visual obstruction reading and initiation date…......... 58

Figure 5: Nest success relative to number of trees within 1-ha………………………… 59

Chapter 3

Figure 1: Study Sites……………………………………………………………………. 89

Figure 2: Potential response to treatment ………………………………………………. 90

Figure 3: Vegetation response to treatment…………………………………………….. 91

Figure 4: Species group response to treatment………………………………………….92

Figure 5: Individual species response to treatment ……………………………………. 94

PREFACE

Each chapter of this dissertation represents a manuscript that is published, submitted, or intended for publication in a specific journal, and formatting within each chapter is thus reflective of those specific journal requirements. Because each of these publications will have one or more coauthors, plural pronouns are used throughout, but as senior author I am responsible for the content of each chapter. Chapter 1, “Grassland birds and patterns of tree avoidance in a highly fragmented landscape” was accepted to the Condor late in 2013. Chapter 2, “The impact of woody vegetation encroachment on waterfowl nest success” was published in Journal of Wildlife Management in 2012. Chapter 3 “Response of grassland birds to experimental tree removal” is intended for submission to the Journal of Applied Ecology in 2014.

INTRODUCTION

Trees and North American grassland ecosystems

Tallgrass prairies were once the most extensive ecosystem in North America, but are now considered by many to be its most endangered (Samson and Knopf 1994). As a result of extensive habitat loss and degradation, grassland-obligate species have experienced consistent and widespread population declines, including birds (Peterjohn and Sauer 1999), small mammals (Horncastle et al. 2005), butterflies (Swengel and Swengel 1999), and snakes (Cagle 2008). Not surprisingly, grassland plants and animals have become a primary target for conservation efforts (Brennan and Kuvlesky 2005, Askins et al. 2007). Declines of grassland fauna are likely the result of extensive habitat loss, but evidence also suggests habitat degradation such as edge effects, lack of disturbance, and encroachment of invasive plants can negatively impact grassland fauna even in large remnant patches (Davis 2004). In particular, the presence of trees within grasslands and the surrounding agricultural matrix has become an issue of conservation concern and efforts to remove or reduce woody vegetation are becoming a management priority in many grassland regions (Herkert 1994, Fulbright 1996, Brennan and Kuvlesky 2005, Kelsey et al. 2006).

Grasslands around the world are experiencing issues with woody vegetation encroachment (Australia, Brown and Carter 1998; Africa, Moleele and Perkins 1998; South America, Dussart et al. 1998; North America, Briggs el al. 2005). In North America, trees have been and continue to be planted in grassland regions with the best of intentions (e.g. see the Homestead Act of 1862). After the American dust bowl of the

1930s, soil conservation efforts focused on planting trees to block wind and thereby slow soil erosion in open, agricultural areas (Salutos 1969). Residents of open areas continue to plant trees around homes for shade and protection from the wind (Salutos 1969, Gardner 2009). Wildlife managers and land owners plant trees to provide habitat for game species such as ring-necked pheasants (*Phasianus colchicus*) and white-tailed deer (*Odocoileus virginianus*).

Once established, trees and shrubs can be difficult to eradicate from grasslands. Unless prescribed burns take place frequently (i.e. every year), fire may not reduce woody plant cover and, in some cases, infrequent fire can promote more rapid expansion of woody vegetation (Clark and Wilson 2001, Lett and Knapp 2005). Most modern grazing techniques fail to slow the progression of woody vegetation and can even promote tree invasion by exposing bare soil (Briggs et al. 2002). Thus, in many cases the only effective way to remove trees or reduce tree encroachment is through labor intensive, mechanical removal. Mechanical removal of trees and shrubs is expensive and is likely to require multiple years of repeated treatment to successfully eradicate trees (Ortmann et al. 1998).

Woody vegetation has the potential to degrade grassland ecosystems through a variety of mechanisms. Trees can cause fundamental changes in the soil chemistry or hydrology of grassland sites that can lead to bottom-up cascades. For example, quick-decaying, nitrogen-rich leaf litter changes soil chemistry and promotes the growth of tree seedlings and other woodland-associated plant species. When this excess nitrogen is combined with shade from adult trees, herbaceous grasses are deterred and tree seedlings grow more quickly. This results in a feedback loop that promotes rapid tree growth (Siemann and Rogers 2003) and can lead to reduced diversity of plants or near elimination of grassland plant species (Briggs et al. 2002, Lett and Knapp 2005).

Alternately, the presence of trees and shrubs in grassland ecosystems can lead to changes in species composition and movement patterns of potential predators. Trees provide habitat niches for predators like American crows (*Corvus brachyrhynchos*) that would otherwise be uncommon in grasslands (Sargeant et al.1993). Woody habitat on grasslands may promote greater densities of generalist predators, such as raccoons (*Procyon lotor*) and Franklin's ground squirrels (*Spermophilus franklinii*) (Sargeant et al. 1993, Renfrew and Ribic 2003). Numerous species like mice and deer that are rarely associated with predation can act as nest predators (Pietz and Granfors 2000, Renfrew et al. 2003). Woody vegetation may also alter foraging behaviors of predators. Trees can provide perches for avian predators or sheltered travel routes for mammalian predators (Lariviere and Messier 2000, Barding 2006) such that the use of habitat near wooded edges would be more perilous for grassland birds. These risks may cause grassland birds to avoid habitat near woody vegetation or risk increased predation of nests, adults, or offspring when they chose territories near wooded areas (Renfrew et al. 2005).

Woody vegetation may also cause changes in the bird community that could be detrimental to grassland birds. Although brown-headed cowbirds (*Molothrus ater*) do not require the presence of trees, they are positively associated with fragmentation and habitat edges and they may utilize trees and shrubs as perches from which to locate host nests (Johnson and Temple 1990). Generalist bird species are more likely to be present on grasslands with woody vegetation and grassland birds may be unable or unwilling to compete with these birds for necessary resources. Further, some generalist and woodland species like common grackles (*Quiscalus quiscula*), blue jays (*Cyanocitta cristata*), house wrens (*Troglodytes aedon*), and gray catbirds (*Dumetella carolinensis*) occasionally act as predators or are known to destroy eggs in nearby nests, and thus an increased abundance of these species can have a direct negative effect on grassland bird fecundity (Sealy 1994).

Finally, it is possible that grassland birds have evolved to avoid wooded habitats and to select open, treeless habitat, even though woody vegetation may not generate any measurable negative impact on grassland bird survival or fecundity. These habitat preferences may have evolved in a time period when there was a clear differentiation between wooded and non-wooded habitat. But in the current landscape of highly fragmented grasslands dotted with woodlots and farms, avoidance of woody habitats may no longer represent a useful behavioral strategy. Grassland birds may not benefit from avoiding wooded habitats or other edges and this avoidance may only serve to limit the amount of habitat available to them (Renfrew and Ribic 2005).

These hypotheses may explain why grassland bird populations are negatively affected as tree abundance increases in grassland habitats. If any of the above hypotheses are true, we should be able to observe measurable outcomes. First, if trees lead to reduced resource availability (either by increasing competition or by degrading available resources) we would expect to see reduced abundance or density of grassland birds on sites with more woody vegetation. We can measure this in the form of reduced abundances of grassland birds or nests. Second, if trees are indicative of increased predation risk or poor quality habitat, we would expect grassland birds to demonstrate reduced fitness, survival, or nest success rates when they utilize more wooded landscapes. Finally, if trees are the underlying cause of reduced grassland bird abundance, we would expect experimental tree-removal to lead to increased abundance or reproductive fitness of grassland birds. In this dissertation I assess how trees influence grassland songbird abundance (chapter 1) and waterfowl nest success (chapter 2) and also examine the impact of experimental tree removal on grassland bird communities (chapter 3).

CHAPTER 1

TREE AVOIDANCE PATTERNS OF GRASSLAND SONGBIRDS

1.1 INTRODUCTION

Declining populations of North American grassland birds are likely driven by extensive loss of grassland habitat (Igl and Johnson 1997, Sauer et al. 2011). Additionally, many remnant and restored prairies across North America are small, isolated, lack fire or grazing disturbances, and are under pressure from invasive species and encroaching woody vegetation (Samson and Knopf 1994). As rural landscapes come under increasing pressure to produce food and energy, grassland management and conservation will need to focus on optimization of available habitat as opportunities to protect or restore additional lands become increasingly scarce (Secchi and Babcock 2007, Fargione 2009).

Trees have been widely planted in grasslands to reduce soil erosion in agricultural regions or protect homes and communities from wind and weather (Tibke 1988). Additionally, humans have planted trees and shrubs on conservation lands to provide shelter for desired game species such as White-tailed Deer (*Odocoileus virginianus*) and Ring-necked Pheasant (*Phasianus colchicus*; Martin 1980, Yahner 1983, Kelsey et al. 2006). The presence of woody vegetation on grasslands can reduce the diversity of native grassland plants, reduce forage quality, alter hydrologic processes, alter predator communities, and reduce grassland carbon sequestration capacity (Grover and Musick 1990, Archer et al. 2001, Jackson et al. 2002, Huxman et al. 2005, Renfrew and Ribic

2008, Ellison et al. 2013). Once trees and shrubs become established, treatments like fire or grazing are unlikely to reverse the progression of woody vegetation. Therefore, maintaining tree-less grasslands generally requires intentional, mechanical tree removal (Briggs et al. 2005). Mechanical removal of established tree groves is expensive and disruptive, often requiring many years and subsequent treatments to successfully eradicate the woody vegetation and regrowth (Quamen 2007, Ellison et al. 2013). Control and removal of lone trees and shrubs is less costly and disruptive, but does require consistent vigilance and effort (S. Vacek, US Fish and Wildlife Service, personal communication).

Grassland bird species have varying preferences or sensitivity to grass type or grassland extent, but avoidance of woody vegetation is relatively consistent for most species and landscapes. Thogmartin et al. (2006) found that forest cover was negatively associated with abundance of several grassland bird species at multiple scales from 800—80,000 ha, and in the case of the Grasshopper Sparrow (*Ammodramus savannarum*), measures of forest cover were more important predictors of abundance than were measures of grass cover. For nine of 10 species of grassland birds in North Dakota, Grant et al. (2004) found that percent woody cover within 500 m of a survey point was the strongest predictor of occurrence. Renfrew and Ribic (2008) noted that Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*) abundance was less sensitive to grassland patch size when tree cover in the area (1200-m buffer) was low, but as tree cover increased both species sought larger core grassland areas. Conversely, different grassland bird species have different preferences for vegetation structure (e.g., grass height, litter depth) and therefore management directed at grass height or litter depth is unlikely to be beneficial for overall grassland bird abundance or diversity (Sample and Mossman 1997). Because most grassland bird species consistently avoid woody vegetation, tree-removal has become a preferred method to improve habitat quality for grassland birds on degraded grasslands (U. S. Fish and Wildlife Service 2003). However, few studies have examined the strength and scale of tree-avoidance with the explicit goal of informing management decisions about tree removal.

Our primary objective was to examine grassland bird density to see if tree avoidance could be discerned in a highly fragmented, habitat-limited environment. If avoidance occurred, we wanted to explore the context and scale of tree avoidance to provide guidance for managers interested in targeted tree-removal that would be most likely to benefit grassland birds. For example, if grassland birds avoid trees at landscape scales, then tree removal in small grassland patches may not affect grassland bird habitat use because woodlots or shelterbelts remain on nearby private lands. Conversely, if grassland birds preferentially select habitat based primarily on local features (e.g., avoiding single trees, selecting for grass height or litter depth), then predictions about habitat preferences based on landscape-level data (e.g., National Land Cover Database; Fry et al. 2011) may be less valuable than on-site assessments of vegetation composition.

1.2 METHODS

Study Area

We conducted point counts on grasslands owned and managed by the U.S. Fish and Wildlife Service in west-central Minnesota, USA. The study area is located in an ecological transition zone between tallgrass prairie to the west and eastern deciduous forest to the east (Ricketts 1999), and thus provides an excellent location for studying gradients of woody vegetation. The landscape surrounding study sites was predominantly row-crop agriculture including corn and soybeans (60%), spring wheat (5%), pasture and hay (4%), and other row crops (3%). The remainder of the landscape was composed of wetlands and restored grasslands (16%), woody vegetation (2%), and developed areas (10%) (Fry et al. 2011).

Exotic grass and forb species such as smooth brome (*Bromus inermis*), sweet clover (*Melilotus* sp.), and alfalfa (*Medicago sativa*) dominated some study sites, whereas others had been restored using native warm-season grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), and numerous native forbs. Common tree species in the region included box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), eastern red-cedar (*Juniperus virginiana*), and eastern cottonwood (*Populus deltoides*). Common shrubs included wild plum (*Prunus americana*) sandbar willow (*Salix interior*), Russian olive (*Elaeagnus angustifolia*), and common buckthorn (*Rhamnus cathartica*). Land managers used a combination of prescribed fire, herbicide, and mechanical removal to control trees and shrubs (USFWS 2003).

Site and Survey Point Selection

We selected study sites with > 20 ha of grassland that maximized variation in woody vegetation in four counties in western Minnesota. To generate point count locations, we used ArcMap 9.0 (ESRI, Redlands, CA) to randomly place points within study sites such that they were ≥ 200 m apart and not located within a wetland or woodlot. Because woodlots and scattered trees made up a small percentage of the landscape (2%), we purposefully added additional point count locations near trees when randomly placed points did not adequately sample these areas.

Point Count Surveys

We conducted 5-minute point count surveys from 30 May–30 June, 2009–2011 during morning hours (0459–1215, only 5% of surveys took place after 1030), on days with winds <40 km/h and without precipitation (Hutto et al. 1986, Ralph et al. 1995). The survey crew consisted of four individuals: two in 2009, one in 2010, and one in 2011. Surveyors counted all birds detected by sight or sound within 100 m, except for birds that were only observed flying overhead (e.g., hawks, swallows). We divided surveys into two distance categories (0–50m and 51–100m) and assigned each bird to a distance bin based on initial detection location (Buckland et al. 2001).

Vegetation Surveys

Vegetation surveys were limited to measurements consistently found to be important in previous studies of grassland bird habitat selection (Fisher and Davis 2010). We assessed vegetation characteristics at the center of each point count area, 25 m north of center, and 25 m south of the center. We measured litter depth to the nearest 0.5 cm (Smith et al. 1995) and grass height and density (i.e. visual obstruction readings (VOR)) to the nearest

0.5 dm (Robel et al. 1970). We used the mean of the three litter and three VOR measurements to generate a single average litter and VOR value for each point count location. Observers also conducted a tree and shrub survey from the center of each point count location. We defined shrubs as perennial woody vegetation 1–4 m in height and trees as perennial woody vegetation > 4 m in height (Thompson et al 2012). Observers counted all shrubs within 50 m and all trees within 100 m; because of their smaller size, shrubs could not be reliably counted beyond 50 m.

Landscape Analysis

We digitized study sites and surrounding regions manually with ArcMap 9.0 using aerial imagery from the first year that a site was surveyed. For sites that we surveyed in more than one year, we examined aerial images annually but found little change in land cover type and utilized a single digitized layer for all years. We categorized land cover as perennial grass (grassland, pasture, hay fields, and ditches), wetland (vegetated wetland and open water), woody vegetation (woodlots, shelterbelts, and large individual trees), crop, or other (i.e., farms, roads, and gravel pits). We used this data layer to generate percent cover statistics for the 100 m radius count circle and areas within 500 m and 1000 m of the count center (i.e., 3.14, 78.5, and 314 ha, respectively). Most grassland bird studies have utilized similar radii or areas; the smallest areas generally describe vegetation within the point count circle and larger areas span from radii of 500 m (Grant et al. 2004), 1000 m (Fletcher and Koford 2002), 1200 m (Renfrew and Ribic 2008), to as large as 1600 m (Bakker et al. 2002, Cunningham and Johnson 2006). To reduce issues of multi-collinearity among habitat categories, we only considered proportion grass and tree and did not include crop, other, or wetland features in any models (reviewed in Graham 2003).

Statistical Analysis

We employed the hierarchical multinomial-Poisson and multinomial-negative binomial mixture models of Royle (2004) and Chandler et al. (2011) as implemented in R (R Foundation for Statistical Computing, Vienna, Austria) with package Unmarked (i.e., modules distsamp and gdistsamp; Fiske and Chandler 2011). This model framework allowed us to account for variables that affected detection rates and concurrently consider covariates that influenced abundance or density (Royle et al. 2004). We used the closed-population formulation of both models, which assumed that birds did not move into or out of the survey area during the 5-minute interval (Buckland et al. 2001).

Spatial autocorrelation was an issue with our study design and a common issue in point count studies (Thogmartin et al. 2004, see review by Dormann et al. 2007). Spatial clustering of survey points and repeated visits can lead to lack of independence of counts within sites. The Unmarked package does not accommodate random effects; however, independence of surveys is assumed to be achieved if the same birds are not counted from multiple survey points. Moreover, non-independence should be revealed by lack-of-fit, and so standard methods for evaluating fit (e.g., parametric bootstrapping) should be useful for assessment of the independence assumption (Royle et al. 2004; J. A. Royle, U.S. Geological Survey, personal communication). Additionally, the negative binomial distribution accounts for some forms of spatial autocorrelation by including an overdispersion term (White and Bennetts 1996).

We truncated extreme values (outliers) and standardized all continuous covariates prior to analysis to facilitate model convergence and reduce bias in parameter estimates (Zuur et al. 2010, Chandler 2012). To identify outliers, we examined histograms of predictor variables; we truncated litter depth at 15 cm (3 measurements), tree and shrub counts at 45 (10 measurements each), and VOR at 8 dm (1 measurement). We imputed missing data for litter depth (n = 3) and VOR (n = 4) using standardized mean covariate values of 0. Proportion grassland within 500 m was strongly correlated with proportion grassland at 1000 m (R^2 = 0.77), as were the proportion of trees at 500 and 1000 m (R^2 = 0.68); thus we did not combine these two spatial scales (500 and 1000 m) in any single model. We noted moderate correlations between variables at 100 and 500 m (R^2 = 0.45 for grass and R^2 = 0.33 for tree), but did not restrict these variables from co-occurring in models. Because primary observers (n = 4) differed among years, year and observer effects were confounded and included together in what we hereafter term year effects.

Model selection.

We began by examining detection functions for each species. We used the half-normal detection function for all species because preliminary assessments showed that of the available options (i.e., half-normal, hazard-rate, uniform, or exponential), the half-normal provided the lowest Akaike's Information Criterion values (AIC; Burnham and Anderson 2002). We then selected detection covariates for each species. We hypothesized that wind (WIND; Beaufort class 1–7), year (YEAR; n = 3), Julian date (DATE; 28 May = 1), cloud cover (SKY; percent of sky that was cloudy), and time of day (TIME; 0500—1230) had the greatest potential to influence detection of birds (TABLE 1). We were concerned that detection rate could be negatively affected by the presence of woody vegetation because woodlots and trees contain a novel community of birds that may distract observers or block visual detections. Thus, we included the proportion of trees within 100 m (PTREE100) as a potential detection covariate. To avoid spurious conclusions about factors influencing detection probability, we used a highly parameterized density model while we assessed support for detection covariates (Survey + Landscape; TABLE 2; Barker et al. 2005). We considered a set of models that included every potential one- or two-covariate combination of detection covariates. We then selected the detection model resulting in the lowest AIC value for each species as the basis for comparing a priori habitat models (Burnham and Anderson 2002). With only two distance bins in our data set, we believe that one- or two-covariate detection models adequately accounted for variation in detection without over-fitting models (Giudice et al. 2012).

After assessing detection covariates, we tested whether the Poisson or negative binomial distribution provided a better model fit for density as determined by lowest AIC value (Royle et al. 2004, Chandler et al. 2011). Also, before proceeding to selection of a priori density models, we examined overall model fit for each species using a parametric bootstrap technique (White et al. 2001). We simulated data (200 iterations) using a highly parameterized density model (Saturated, TABLE 2) and then re-fit the model to the simulated data. This generated a sampling distribution of $\chi2$ statistics that could be compared to the $\chi2$ value from the original model (Fiske and Chandler 2011). We assumed adequate model fit when tests comparing these statistics resulted in a p-value > 0.05.

We considered seven a priori models to describe potential preference for grass and/or avoidance of woody vegetation (Burnham and Anderson 2002; TABLE 2). We focused on percent grass cover within concentric circles to avoid the issue of patch delineation. We hypothesized that suitable habitat (grass) and hostile habitat (trees) were the most important drivers of habitat selection and focused on modeling these features exclusively. Preliminary examination of scatterplots and loess curves did not reveal any compelling evidence for non-linear patterns (Zuur 2010) and thus we did not consider quadratic or cubic terms.

We included the proportion of the point count area (100-m radius) composed of grass (PGRASS100) in every model to account for survey areas that were not entirely composed of suitable habitat for grassland birds (e.g., open water, crop fields). We considered three models that examined support for three separate scales of habitat measurement that included grass and woody vegetation descriptors: Survey-point (100 m), Patch (500 m), and Landscape (1000 m). Two additional models contained variables combining both grass and woody vegetation descriptors from more than one scale; Survey + Patch and Survey + Landscape. Finally, the last two models contained only grass or only tree-related variables (Grass only, Tree only) from multiple scales (Survey-point and Landscape). We compared support for models using AIC (Burnham and Anderson 2002).

We generated model-based predictions for each species with the top-ranked model. When comparing the impact of grass-related versus woody vegetation-related covariates, we varied all covariates in one group (e.g., grass-related) from the 10th to

90th percentile while holding the covariates in the other group (e.g., tree-related) at average values. For example, if the top model was Survey + Patch, predictions examining the impact of grass-related descriptors would increase VOR, LITTER and PGRASS500 from 10th—90th percentile while SUMSHRUB, SUMTREE, PTREE100, and PTREE500 would be held at average values. In all predictions, we held PGRASS100 and any detection covariates constant at average values. When YEAR was a supported detection covariate, we selected the year with the median detection value. Numbers in parentheses represent 95% confidence intervals unless otherwise noted.

1.3 RESULTS

During 2009–2011, we conducted 446 point counts on 35 grassland sites with an average of 8.9 point counts per site per year (range: 2—20). We visited 24 sites one year, seven in two years and four sites in three years of the study. The most frequently observed grassland birds were Clay-colored Sparrow (*Spizella pallida*, n = 570), Bobolink (n = 478), Sedge Wren (*Cistothorus platensis*, n = 443), and Savannah Sparrow (n = 255). Other frequently observed species included Red-winged Blackbird (*Agelaius phoeniceus*, n = 1008), Common Yellowthroat (*Geothlypis trichas*, n = 533), Common Grackle (*Quiscalus quiscula*, n = 363), and Yellow Warbler (*Setophaga petechia*, n = 175).

Bobolink

Apparent Bobolink density was 0.34 ha^{-1} (σ^2 = 0.63; range = 0–2.87 birds ha^{-1}). Four detection covariates improved model fit; DATE and SKY negatively influenced detection probability, TIME had a positive influence, and detection probability varied by YEAR.

Combinations of detection covariates did not produce a better model fit than DATE alone. The negative binomial distribution provided better fit than the Poisson-structured model (ΔAIC = 8.49) and the goodness of fit test indicated adequate model fit with the negative binomial distribution (p = 0.13). The top model was Survey + Patch followed by Survey + Landscape (ΔAIC = 2.78, TABLE 3; TABLE 4; FIGURE 1). Other models performed poorly in comparison (ΔAIC > 19).

The best supported model predicted 0.54 Bobolinks ha^{-1} (0.44–0.66) at mean covariate values. Bobolink detection probabilities ranged from 0.677 (0.546–0.782) for early surveys (2 June, 10th percentile) to 0.344 (0.276–0.419) for late surveys (22 June). The top model predicted Bobolink density to decrease from 0.86 (0.69–1.07) to 0.21 ha^{-1} (0.15–0.32) as woody vegetation increased from the 10th to 90th percentile (FIGURE 2 solid line). Bobolink density increased from 0.30 (0.22–0.42) to 0.98 (0.73–1.31) as grass-related covariates increased from the 10th to 90th percentile (TABLE 1; FIGURE 2 dashed line).

Clay-colored Sparrow

Clay-colored Sparrow mean apparent density was 0.56 ha^{-1} (σ^2 = 0.03, range = 0–2.23). DATE (positive), WIND (negative), and YEAR influenced detection probability. The best model for detection included both YEAR and DATE. The Poisson distribution fit better than a negative binomial (ΔAIC = 2.00) and the saturated model fit data well (p = 0.36). The best supported Clay-colored Sparrow density model was Survey + Landscape, but Survey + Patch performed similarly (ΔAIC = 2.01, TABLE 3; TABLE 4; FIGURE 1).

The best supported model predicted 0.56 Clay-colored Sparrows ha^{-1} (0.46–0.67) at mean covariate values. Detection rates varied by year and increased with Julian date (β = 0.154; SE = 0.070); detection rates increased throughout the season from 0.47 (0.20–0.70; 2 Jun) to 0.85 (0.64–0.94; 22 Jun) during the year with the highest detection probability (2010). In 2011, the year with the lowest estimated detection probability, detection increased from 0.50 (0.34–0.65) to 0.71 (0.53–0.83) during the same time period. Clay-colored Sparrow density increased from 0.52 (0.42–0.63) to 0.65 (0.52–0.82) as woody vegetation covariates increased (FIGURE 2). Density also increased from 0.44 (0.34–0.58) to 0.73 (0.56–0.94; FIGURE 2) as grass-related covariates increased.

Savannah Sparrow

The mean apparent density of Savannah Sparrows was 0.18 ha^{-1} (σ^2 = 0.31, range = 0–1.59). Detection probability varied by YEAR and the proportion of point count area composed of woody vegetation (PTREE100) had a marginal, negative influence on detection (the model including PTREE100 scored 0.41 AIC units lower than the null detection model). The best detection model ultimately included only YEAR. A negative binomial distribution fit data better than the Poisson distribution (ΔAIC = 24.45) and provided sufficient model fit (p = 0.21). The best supported density model was Survey + Patch followed by Survey + Landscape (ΔAIC = 2.49, TABLE 3; TABLE 4; FIGURE 1).

The best supported model predicted 0.38 Savannah Sparrows ha^{-1} (0.29–0.50) at mean covariate values. Detection probability varied annually, ranging from a high of 0.52 (0.37–0.66) in 2011 to a low of 0.33 (0.25–0.42) in 2010. Savannah Sparrow density decreased from 0.70 (0.52–0.93) to 0.12 (0.07–0.21) as woody vegetation covariates increased (FIGURE 2, solid line). Density decreased from 0.52 (0.33–0.81) to 0.47 (0.30–0.73) as grass-related covariates increased (Fig 2, dashed line).

Sedge Wren

The mean apparent density of Sedge Wrens was 0.32 (σ^2 = 0.49, range = 0–1.91). We noted that most Sedge Wrens arrived late during the 2011 breeding season and to account for this we tested an interaction of DATE and YEAR in the density model. The interaction was highly supported (ΔAIC = 64.56) and we included it in all further models. Only WIND significantly improved detection model fit and it negatively influenced detection. The negative binomial distribution fit data better than the Poisson distribution (ΔAIC = 4.16). The saturated model with a negative binomial structure adequately fit the data (p = 0.21). The best supported model was Survey + Landscape (TABLE 3; TABLE 4; FIGURE 1).

Predicted density varied from 0.49 Sedge Wrens ha^{-1} in 2009 (0.37–0.65), to 0.72 ha^{-1} in 2010 (0.57–0.92), and 0.16 ha^{-1} in 2011 (95% CI: 0.10–0.26). Detection probability decreased from 0.57 (0.46–0.67) at low wind speeds (Beaufort scale 0) to 0.45 (0.37–0.53) at higher wind speeds (Beaufort scale 3). Density decreased from 0.79 (0.60–1.04) to 0.23 (0.15–0.37) as woody vegetation covariates increased (FIGURE 2 solid line). Density increased moderately as grass-related covariates increased ($\hat{N}$10th percentile = 0.44, 95% CI: 0.30–0.65 and $\hat{N}$90th percentile = 0.53, 95% CI: 0.38–0.75; FIGURE 2 dashed line).

1.4 DISCUSSION

Detection probability

Density estimates can be biased by incomplete detection of birds (Buckland et al. 2001). A variety of new methods and programs have made adjusting for imperfect detection more tenable than in the past (Anderson 2001, White 2005, Fiske and Chandler 2011). In our study, we estimated mean cumulative detection probability within the 100m radius to be between 0.33–0.85. Lueders et al. (2006) reported cumulative detection probabilities between 0.76–1.00 for grassland songbird species in mixed-grass prairies that were surveyed using a 100-m radius point count and analyzed with distance methods. Jacobs et al. (2012), also using 100-m radius count and distance methods, reported cumulative detection rates between 0.118–0.237 for grassland songbirds in Missouri and Diefenbach et al. (2003) reported rates between 0.57–1.00 for grassland songbird species along transect routes. We found that wind, date, and year/observer were the primary factors influencing detection probability; this is consistent with other studies that have assessed detection.

Preference for grass or avoidance of woody vegetation?

Our results are generally consistent with other studies that examined the effects of woody patches on local-scale density of grassland birds in both fragmented (e.g., Grant et al. 2004, Renfrew and Ribic 2008) and relatively intact landscapes (Cunningham and Johnson 2006). We predicted that grassland bird density would generally increase with grassland extent, litter depth, and vegetation height and density (VOR) (Horn and Koford 2000, Davis 2004, Grant et al. 2004, Murray et al. 2008), and that more shrubs and trees at all scales would negatively influence density (Bakker 2003, Grant et al. 2004, Graves et al. 2010). Bobolinks demonstrated habitat associations that entirely followed those predictions (FIGURE 2). Sedge Wrens also generally followed our predictions with overall increasing density when all grass covariates were increased and decreasing density as woody vegetation increased (FIGURE 2).

Clay-colored Sparrows showed a similar positive association with all grass metrics and were negatively associated with local tree counts. However, Clay-colored Sparrow density was positively associated with shrub counts and percent tree cover within 100 and 1000 m, resulting in a neutral response to increases in woody vegetation (FIGURE 2). Even though Clay-colored Sparrows are a grassland-dependent species, they nest in shrubs and thus prefer some available shrub cover, so and it is not surprising that they would have a complex association with shrubs and trees (Arnold and Higgins 1986, Dechant et al. 2003a). Savannah Sparrow density was negatively influenced by all woody vegetation metrics in the top model, but was also negatively associated with greater proportion grassland (500 m), litter depth, and VOR. The negative relationship with increasing grass-related covariates (FIGURE 2) was largely driven by a strong negative relationship with grass height and density (VOR) and when we fixed the VOR value at -1 (1 SD below the mean with other grass-related covariates increasing from 10th to 90th percentiles) the model predicted a negligible decline in Savannah Sparrow density when increasing grass values. In southern Wisconsin, Savannah Sparrow density was also negatively associated with vegetation height and density (Sample 1989); but other studies have found them to be positively associated with vegetation height (Bollinger 1995) or found no clear response (Davis 2004, Winter et al. 2005). These differences may be due to regional variation in what constitutes a relatively high or low VOR measurement.

Some grass-related variables described physical qualities of grass (LITTER and VOR) while others described extent of grass at concentric scales (PGRASS 100, 500, or 1000). We expected the four species to show some variation in response to physical qualities of grass, but we were surprised to also find a mixed response to measures of grass extent. As expected, all species demonstrated strong positive associations to increasing grass at the 100-m scale. Bobolink and Clay-colored Sparrow densities were also positively associated with grass at 500 m and 1000 m radii, respectively. However, Savannah Sparrow density decreased with increasing grass at the 500-m scale and Sedge Wren density decreased with increasing grass at the 1000-m scale. Given the tendency of grassland songbirds to exhibit area sensitivity, it is counter-intuitive that a location with more surrounding grassland would be associated with lower densities of some grassland bird species (Johnson and Igl 2001, Ribic et al. 2009). In the case of Sedge Wrens, one explanation is that more extensive grass cover may have been associated with fewer wetland edges, which is a preferred habitat for this species (Dechant et al. 2003b). A more general explanation for this mixed response is that grass at large spatial scales was positively correlated with woody vegetation and that tree-avoidance is a potentially more important driver of habitat selection than grassland extent. Proportion of grass at 500-m and 1000-m scales was positively correlated with woody vegetation covariates for 7 of 10 combinations (r_{max} = 0.33). In this region, landscapes with the fewest trees were usually dominated by agriculture and often contained very little grassland. Landscapes with more extensive grasslands were often in areas that were generally less suitable for agriculture (e.g., steep slopes, poor soils, near riparian areas). For a variety of reasons, these largely unmanaged grasslands tended to contain more woody vegetation (e.g., from intentional planting, encroachment, or due to proximity to wooded riparian zones).

Other than the mixed response of Clay-colored Sparrows to woody vegetation, all other species showed consistent negative associations with all woody vegetation covariates. Additionally, the tree-only model was much more highly supported than the grass-only model for Bobolink, Savannah Sparrow, and Sedge Wren. This again suggests that when selecting habitat, these species may be more motivated by tree-avoidance than by attraction to grass extent or type, at least for the specific variables that we measured. For Savannah Sparrow and Bobolink, top models predict that reducing woody cover within 100 m would be more effective for increasing bird density than almost any reasonable increase in grass at the 500 or 1000 m scales. We used top models to predict the effects of reducing fine-scale woody vegetation from average values to minimum values (removing 4.3 shrubs from within 50 m, 4.7 trees within 100 m, and 628 m2 of woodlot from the surrounding 100m). In doing so, models predicted increases in Bobolink, Savannah Sparrow, and Sedge Wren density. However, increasing grass within 500 m by 11.6 ha (one SD over mean) or 23.4 ha (two SD over mean) led to smaller predicted increases in Bobolinks and did not lead to any predicted increases for Savannah Sparrows or Sedge Wrens.

Scales of Habitat Preference

Best supported models for each of the four species in our study included grass and tree variables at multiple scales (Survey + Patch and Survey + Landscape). For Savannah Sparrow, Bobolink, and Clay-colored sparrow, the two multiple-scale models received similar support and represented the top two models for each species, suggesting that the two larger scales (i.e., 500m and 1000m radii) provided similar information on habitat quality for these species. For these three species, the finest-scale model (i.e., Survey-point) was given the most support of models that incorporated a single scale (Survey-point, Patch, or Landscape; TABLE 3).

Sedge Wrens demonstrated a different pattern. The two best supported density models for Sedge Wrens were Survey + Landscape and Tree-only (ΔAIC = 8.87, TABLE 3). Even though the parameters included in the models Survey + Patch and Survey + Landscape were very similar, the Survey + Patch model ranked 25 AIC units lower. Landscape was the highest ranked single-scale model for Sedge Wrens; again indicating a preference for models that incorporate the 1000-m scale. Bakker et al. (2002; South Dakota), Fletcher and Koford (2002; Iowa), and Cunningham and Johnson (2006; North Dakota) also noted that Sedge Wrens selected habitat at broader, landscape-scales. All of these studies report associations with larger landscapes, but ours appears to be the only study reporting a negative association between Sedge Wren abundance and grassland cover.

Despite sharing similar vegetation preferences to the other species, Sedge Wren density was more strongly associated with landscape-level features. Sedge Wren presence and density is often associated with wetland availability and specifically wet meadow habitats (Dechant et al. 2003b). In dry years or in areas with few wet meadows, Sedge Wrens may preferentially select areas that contain at least some wet meadow and wetland habitat (i.e., small scale). The Palmer Modified Drought Index (PMDI; Mo and Chelliah 2006) for 2010 and 2011 suggested moderate to extremely wet conditions in our study area. As a result, the region experienced greater wetland availability and more lush upland growth than average years. In response to this increase in availability of favorable habitat, Sedge Wrens may have responded by selecting habitat at broad scales.

The remaining grassland patches in western Minnesota are, for the most part, publically owned. These grasslands exist within a mosaic of private land that complicates endeavors to manage for grassland bird populations. Grassland management thus tends to occur primarily at the local or patch scale, and the greater landscape is largely excluded from management actions like tree removal. Even though local vegetation characteristics did influence grassland bird density in our study, these fine-scale habitat preferences were variable by species and we can therefore expect management aimed at these qualities to benefit only some species. The grassland species included in this study responded to woody vegetation and grassland metrics at larger scales than those generally encompassed in a management unit. Because density was influenced by trees at 500-1000m scales, we can expect that the removal of lone trees or singular woodlots is not likely to lead to a measurable increase in grassland bird density. We may find that grassland birds respond unexpectedly to management actions, particularly those that occur only at smaller scales. Tree removal without consideration of landscape context may lead to treatments that have little benefit for grassland birds and ultimately may not help to reach conservation goals.

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TABLE 1

Description of variables used to model detection and density for four species of grassland songbirds. We conducted point count surveys (n = 446) from 2009–2011 in west-central Minnesota. Variables VOR through PTREE1000 affected habitat selection and therefore influenced bird density and variables DATE through TIME potentially influenced detection rates of birds. Columns labeled 10th, 50th and 90th represent percentiles.

Covariate	**Description**	**Min.**	**10th**	**50th**	**Mean**	**90th**	**Max.**
VOR	Visual obstruction reading (dm)	0	1.2	2.4	2.5	3.8	15.7
LITTER	Litter depth (cm)	0	1.9	5.2	5.4	9	36.3
SUMSHRUB	Count of shrubs within 50m	0	0	0	4.3	15	104
SUMTREE	Count of trees within 100m	0	0	0	4.7	13	70
PGRASS100	Proportion grass within 100m	0.32	0.51	0.83	0.79	0.98	1.00
PGRASS500	Proportion grass within 500m	0.16	0.254	0.44	0.45	0.65	0.93
PGRASS1000	Proportion grass within 1000m	0.08	0.16	0.27	0.30	0.48	0.67
PTREE100	Proportion tree cover within 100m	0.00	0.00	0.00	0.02	0.07	0.39
PTREE500	Proportion tree cover within 500m	0.00	0.00	0.02	0.03	0.07	0.12
PTREE1000	Proportion tree cover within 1000m	0.00	0.00	0.03	0.029	0.06	0.14
$DATE_a$	Date(1 = May 29)	29 May	3 Jun	12 Jun	13 Jun	23 Jun	30 Jun
WIND	Beaufort wind speed	0	0	2		3	6
$YEAR_a$	Year	*n=3*	-	-	-	-	-
SKY	% cloud cover	0	0	50	50.8	100	100
TIME	Initiation time of survey	459	631	757	836	1013	1215

a For Sedge Wrens, DATE and YEAR were also considered in abundance models

TABLE 2

A priori model structures for comparing grassland songbird density in relation to habitat characteristics. We included percent grass at the 100-m scale in all models to account for point count areas that were not entirely composed of grass. We used the saturated model to assess overall model fit, but this model was not considered in model selection procedures. See Table 1 for a description of covariates.

Model name	**Covariate structure**
Survey-point	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100
Patch	PGRASS500 + PTREE500
Landscape	PTREE1K + PGRASS1K
Survey + Patch	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100 + PGRASS500 + PTREE500
Survey + Landscape	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100 + PGRASS1K + PTREE1K
Grass only	VOR + LITTER + PGRASS1K
Tree only	SUMSHRUB + SUMTREE + PTREE100 + PTREE1K
Saturated	PGRASS100 + PGRASS100^2 + LITTER + VOR + SUMSHRUB + SUMTREE + SUMTREE^2 + PTREE100 + PTREE100^2 + PTREE500 + PTREE1K + PGRASS500 + PGRASS1K + PGRASS1K × SUMTREE + PGRASS1K × PTREE1K

TABLE 3

Model results including ΔAIC, number of parameters (k), and model weight (Wt) from models of abundance for four species of grassland birds surveyed during 446 point counts in western Minnesota, 2009–2011. Models included variables from 3 scales: survey (100-m radius), patch (500-m radius), and landscape (1000-m radius). At each scale, variables described characteristics of woody vegetation or grass quantity or quality. Bold font indicates model set changing to new species and top model for that species.

Species	Model	k	ΔAIC[b]	W_t
Bobolink	**Survey + Patch**	**12**	**0.00**	**0.800**
Negative Binomial	Survey + Landscape	12	2.78	0.200
Detection model: DATE	Survey-point	10	19.15	0.000
	Tree only	9	27.43	0.000
	Patch	7	31.05	0.000
	Landscape	7	38.80	0.000
	Grass only	8	45.59	0.000
	Detection	4	96.17	0.000
	Null	3	114.82	0.000
Clay-colored Sparrow	**Survey + Landscape**	**13**	**0.00**	**0.473**
Poisson	Survey + Patch	13	2.01	0.173
Detection model:	Grass only	9	2.58	0.130
DATE + YEAR	Survey-point	11	2.95	0.108
	Tree only	10	3.77	0.072
	Landscape	8	5.34	0.033
	Patch	8	7.44	0.012
	Detection	5	59.91	0.000
	Null	2	76.92	0.000
Savannah Sparrow	**Survey + Patch**	**13**	**0.00**	**0.724**
Negative Binomial	Survey + Landscape	13	2.49	0.208
Detection model: YEAR	Tree only	10	5.13	0.056
	Survey-point	11	8.32	0.011
	Patch	8	12.87	0.001
	Landscape	8	17.75	0.000
	Grass only	9	27.46	0.000
	Detection	5	37.53	0.000
	Null	3	38.98	0.000
Sedge Wren	**Survey + Landscape**$_a$	**17**	**0.00**	**0.990**
Negative Binomial	Tree only$_a$	14	8.87	0.012

Detection model: WIND	Landscape[a]	12	13.61	0.001
	Survey-point[a]	15	22.18	0.000
	Survey + Patch[a]	17	25.44	0.000
	Grass only[a]	13	31.44	0.000
	Patch[a]	12	86.77	0.000
	Null	3	114.27	0.000
	Detection[a]	4	115.72	0.000

a. Sedge Wren a priori model set included an interaction of DATE×YEAR in the abundance model to account for late arrival of the species to breeding grounds in 2011.

b. AIC score for the top models: Bobolink = 1337.24, Clay-colored Sparrow = 1781.54, Savannah Sparrow = 1047.1, and Sedge Wren = 1323.04

TABLE 4

Covariate coefficient estimates (β) and standard errors (SE) for variables affecting detection rates (p) and density (λ) of four grassland bird species in Minnesota, 2009–2011. Estimates are based on the best supported model for each species.

	Bobolink		Clay-colored Sparrow		Savannah Sparrow		Sedge Wren	
Covariate	β	SE	β	SE	B	SE	β	SE
Intercept (p)	4.055	0.076	4.255	0.125	3.760	0.080	4.024	0.070
DATE (p)	− 0.226	0.049	0.154	0.070	-	-	-	-
$YEAR_{2010}$ (p)	-	-	0.341	0.167	–0.026	0.093	-	-
$YEAR_{2011}$ (p)	-	-	– 0.037	0.135	0.298	0.132	-	-
WIND (p)	-	-	-	-	-	-	– 0.083	0.035
Intercept (λ)	– 0.613	0.102	– 0.581	0.095	– 0.962	0.134	– 0.712	0.142
DATE (λ)	-	-	-	-	-	-	– 0.365	0.091
$YEAR_{2010}$ (λ)	-	-	-	-	-	-	0.390	0.138
$YEAR_{2011}$ (λ)	-	-	-	-	-	-	– 1.089	0.254
PGRASS100 (λ)	0.318	0.070	0.322	0.053	0.210	0.100	0.319	0.063
VOR (λ)	0.138	0.060	0.112	0.046	− 0.261	0.091	0.181	0.059
LITTER (λ)	0.142	0.052	– 0.005	0.047	0.009	0.086	0.049	0.057
PGRASS500 (λ)	0.191	0.058	-	-	− 0.047	0.090	-	-
PGRASS1000 (λ)	-	-	0.097	0.045	-	-	– 0.124	0.061
SUMSHRUB (λ)	– 0.231	0.092	0.129	0.045	− 0.261	0.091	– 0.081	0.100
SUMTREE (λ)	− 0.177	0.079	− 0.009	0.047	− 0.216	0.122	– 0.099	0.075
PTREE100 (λ)	− 0.118	0.088	0.018	0.055	− 0.189	0.142	– 0.202	0.088
PTREE500 (λ)	− 0.231	0.063	-	-	− 0.339	0.102	-	-
PTREE1000 (λ)	-	-	0.030	0.040	-	-	– 0.308	0.077
$YEAR_{2010}$×DATE (λ)	-	-	-	-	-	-	0.321	0.115
$YEAR_{2011}$×DATE (λ)	-	-	-	-	-	-	1.049	0.203

FIGURE 1. Expected change in density for four species of grassland songbirds when varying single covariates from the best-supported model (all other values held at mean). We generated predictions by varying the covariate of interest from the 5th–95th percentile. The vertical dotted line represents the mean value for the variable denoted on the x-axis and gray lines represent 95% confidence intervals.

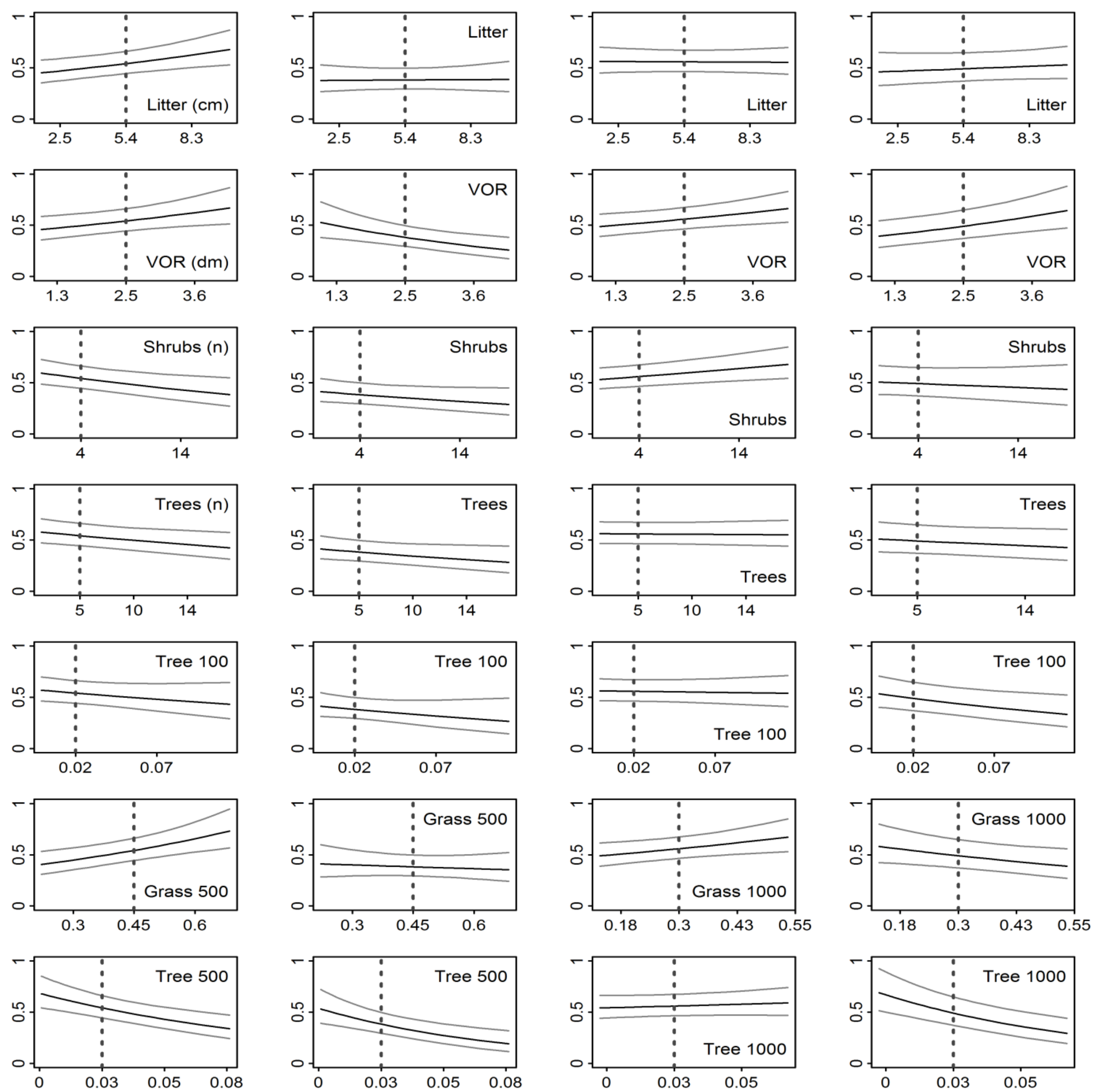
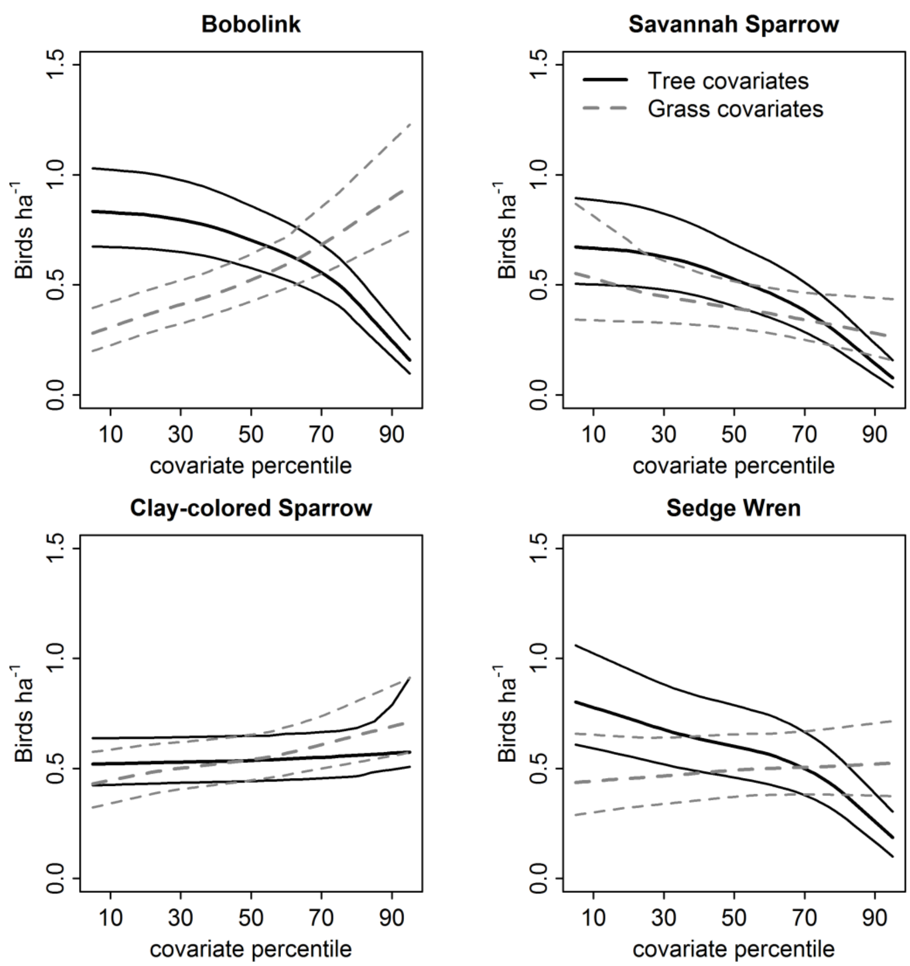


FIGURE 2. Plots comparing the effect of increasing grass variables (dashed lines; VOR, LITTER, and GRASS500 or GRASS1000) to increasing woody vegetation variables (solid lines; SUMSHRUB, SUMTREE, PTREE100, and PTREE500 or PTREE1000). Results are based on top models for four grassland bird species from 446 point count surveys conducted in western Minnesota, 2009-2011.



CHAPTER 2

IMPACT OF ENCROACHING WOODY VEGETATION ON NEST SUCCESS OF UPLAND NESTING WATERFOWL

2.1 INTRODUCTION

Grasslands are one of the most critically endangered ecosystems in North America, with estimates of 79% loss across the continent (Samson and Knopf 1994, Noss et al. 1995). Minnesota has lost >99% of its native tallgrass prairie, primarily through conversion to row-crop agriculture (Samson and Knopf 1994). Remnant and restored grasslands are often further degraded because of isolation, fragmentation, fire suppression, invasive plants, and encroachment by woody vegetation (Samson and Knopf 1994). Historical prairie regions have experienced considerable increases in woody cover (Bragg and Hulbert 1976, Samson and Knopf 1994), owing in large part to human activity, such as planting of woodlots and shelterbelts (Droze 1977). Many additional anthropogenic factors including interruption of disturbance regimes (fire, grazing), increases in atmospheric carbon, and long-term climate change have been implicated in the continued spread and establishment of woody vegetation in grassland areas (Johnson et al. 1993, Heisler et al. 2003).

Numerous studies suggest that encroaching woody vegetation can negatively affect grassland-associated passerine birds. Grant et al. (2004) found that 11 of 15 species of grassland songbirds in North Dakota declined in abundance as woody vegetation increased, and that vesper sparrows (*Pooecetes gramineus*) and clay-colored sparrows (*Spizella pallida*) experienced reduced nest survival when nesting in more wooded areas

(Grant et al. 2006). In western Minnesota, Johnson and Temple (1990) found that nest predation and brood parasitism rates were lower for songbird nests in large grassland patches that were far from wooded edges. Additionally, grassland songbirds in Wisconsin avoided placing nests near edges (both wooded and non-wooded), but nest success did not differ by distance from edge (Renfrew et al. 2005).

Nest success is often the most influential determinant of population change in prairie-nesting waterfowl (Cowardin and Johnson 1979, Hoekman et al. 2002), so factors that affect nest survival are of utmost concern to waterfowl managers. Few studies in primary literature have examined waterfowl nest survival in relation to encroaching woody vegetation, even though many grassland areas are managed specifically for waterfowl. Recent evidence from the Canadian Prairie-Parklands suggests that waterfowl nesting success in aspen-dominated parkland is less than in adjacent mixed-grass prairie (Arnold et al. 2007), but this study contrasted nest success across adjacent biomes and did not examine encroachment of woody vegetation into former grassland areas. Gazda et al. (2002) found that waterfowl nest success was lower on grasslands with higher levels of invasion by Russian olive (*Elaegnus angustifoli*); and although they suspected avian predators, an experimental removal of trees did not reduce the abundance of the most common avian nest predator, black-billed magpies (*Pica hudsonia*).

Encroachment of woody vegetation could affect waterfowl nest survival through a variety of mechanisms. Trees can provide habitat niches for predators that might not otherwise inhabit the local landscape, including American crows (*Corvus brachyrhynchos*), great horned owls (*Bubo virginianus*), and red-tailed hawks (*Buteo* *jamaicensis*; Sargeant et al. 1993). Additionally, woody habitat may promote greater densities of certain predators, such as raccoons (*Procyon lotor*) and Franklin's ground squirrels (*Spermophilus franklinii*), even if woody vegetation is not essential for their presence (Sargeant et al. 1993, Renfrew and Ribic 2003). Finally, woody vegetation may alter foraging behaviors of predators, such as avian predators using trees as lookouts or mammalian predators using shelterbelts as travel lanes (Larivière and Messier 2000), so that nests located adjacent to woody vegetation are more likely to be depredated.

Our primary objective was to test the hypothesis that encroaching woody vegetation affects nest survival of upland-nesting ducks. As a secondary objective, we sought to identify other variables such as amount and density of grassland habitat, density and proximity of wetland habitat, and other pertinent factors that might influence duck nest survival on managed grasslands.

2.2 STUDY AREA

We conducted our study on Waterfowl Production Areas (WPAs) in the Morris Wetland Management District along the eastern edge of the Prairie Pothole Region in Big Stone, Stevens, Traverse, and Swift counties, Minnesota, USA. This area has experienced extensive wetland drainage and conversion of native grasslands to high-intensity agriculture. The landscape of these 4 counties was dominated by agriculture including corn and soybeans (60%), spring wheat (5%), pasture and hay (4%), and other row crops (3%). Wetlands and restored grasslands (16%), developed areas (10%), and woody vegetation (1–2%) comprised the remainder (United States Department of Agriculture, National Land Cover Database, http://datagateway.nrcs.usda.gov, accessed on 8 Dec. 2011).

We focused on WPAs in landscapes with predicted waterfowl densities of >15 breeding duck pairs/km^2 (http://www.fws.gov/midwest/hapet/ThunderStormMaps.html, accessed on 1 Mar. 2008). We excluded sites that received cover management (burning, mowing, or grazing) within the previous 12 months (Devries and Armstrong 2011) as well as sites with <20 ha of upland cover. We selected 14–16 study sites each year with an effort to maximize variation in the amount of woody vegetation. To help discriminate between site and year effects, we studied 6 sites ≥2 years. Although we lacked experimental control, we used WPAs where trees had been removed through recent management efforts or that were slated for future tree removal. For example, Rothi WPA had undergone a large-scale woodlot removal in 2003–2004 and Geyer WPA had several large woodlots removed in the fall of 2010 after completion of our study. Waterfowl Production Areas chosen as study sites varied widely in size ($\bar{x}$ = 175 ha, range = 32–505 ha), management history, and extent of woody vegetation ($\bar{x}$ = 2.9% range = 0.3–15.1% woody vegetation cover within the 800-m site area, see methods). Vegetation varied from sites dominated by exotics including smooth brome (*Bromus inermis*), alfalfa (*Medicago sativa*), and sweet clover (*Melilotus* sp.) to diverse patches of native grasses and forbs dominated by big bluestem (*Andropogon gerardii*), little bluestem, (*Schizachyrium scoparium*), switch grass *(Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and sideoats gramma (*Bouteloua curtipendula*).

Previous efforts to manage woody vegetation within Morris Wetland Management District included prescribed burning, haying, and grazing. Additionally, managers removed scattered trees with chainsaws or machine-mounted shears, whereas removal of large woodlots involved a combination of chainsaws, machine-mounted shears, and machine tree shredders. For a number of years after removal, tree regrowth was managed with fire or herbicide. Managers targeted tree species that were invasive either regionally or in the absence of fire. Common tree species in the district included box elder (*Acer negundo*), eastern cottonwood (*Populus deltoides*), eastern red-cedar (*Juniperus virginiana*), green ash *(Fraxinus pennsylvanica*), various willows (*Salix* spp.), and the invasive/exotic Siberian elm (*Ulmus pumila*). Managers actively controlled against native shrubs including wild plum (*Prunus americana*), sandbar willow (*Salix interior*), and redosier dogwood (*Cornus sericea*) as well as non-native shrub species including Russian olive (*Elaeagnus angustifolia*) and buckthorn (*Rhamnus cathartica*).

2.3 METHODS

Data Collection

We searched for nests on 15–60 ha of upland habitat at each site; crews were able to search larger areas on sites with fewer duck nests and sites with more extensive upland. We searched 5 sites in all 3 years, 1 site in 2008 and 2010, and the remaining 27 sites in a single year from 28 April–15 July between 0800–1400 hours (Gloutney et al. 1993). Three-person crews (2 drivers, 1 spotter) dragged a 75-m chain between 2 vehicles to locate nests by flushing attendant females (Klett et al. 1986). Once we located a nest, we marked its location with a Global Positioning System and placed a 1-m stake with numbered orange flagging 2 m north of the nest bowl. At nests, we recorded the number of eggs and estimated incubation stage by candling ≥2 eggs at discovery and at any subsequent visit until the nest was destroyed, abandoned, or hatched (Weller 1956). We estimated initiation date by backdating based on clutch size and incubation stage assuming birds laid 1 egg per day. We revisited nests every 5–14 ($\bar{x}$ = 10.1) days and categorized a nest as successful when ≥1 egg hatched as evidenced by ≥1 duckling present or intact membranes at the nest, destroyed when nest evidence indicated predation, or abandoned when eggs in an unattended nest showed no advance in incubation stage (Klett et al. 1986, Shaffer et al. 2004). If a nest was partially depredated and then abandoned, we considered it abandoned if >0.5 of the clutch was left intact, otherwise it was considered depredated (Ackerman et al. 2003). We noted any other outcomes including failure by flooding, mowing, or infertile eggs. We excluded nests that were damaged by investigators, abandoned in the first visitation interval following discovery, or destroyed before discovery from analysis (Klett et al. 1986). We included nests that were abandoned for reasons other than investigator disturbance in analyses and treated them as failed nests. The University of Minnesota approved all field methods (Institutional Animal Care and Use Committee protocol 0903A61081).

In 2009 and 2010, we recorded a visual obstruction reading (VOR; McKinnon and Duncan 1999) during the terminal nest visit. We took measurements by placing a pole just north of the nest bowl and recording obstruction to the nearest 0.5 dm from 4 m away at 1 m height in each cardinal direction (Robel et al. 1970). We averaged 4 recordings to generate a VOR metric. Because we did not take these measurements in

2008, we standardized 2009 and 2010 VOR readings ($\bar{x}$ = 0, SD = 1) and assigned values of 0 to all 2008 nests. To ensure that this did not affect model selection or final model estimates, we excluded 2008 data and verified that we obtained similar results in all cases. Unless otherwise noted, we converted VOR values back to normal visual obstruction (i.e., units in dm, not standardized) readings within text and figures.

At each nest site, we measured proximity and amount of woody vegetation within a 56-m radius (1-ha circle). We defined shrubs as woody vegetation 1–4 m tall, trees as woody vegetation >4 m tall, and woodlots as groups of closely-spaced (i.e., merged canopy) trees making up ≥0.1 ha. The distinction between shrubs and trees was somewhat arbitrary, but it was designed to separate species like plum, dogwood, Russian olive, and buckthorn, which rarely get above 4 m tall in open grassland, from tree species like box elder, Siberian elm, and cottonwood, which regularly exceeded this height. We used a rangefinder to measure distance from a nest to the nearest shrub and tree. We truncated measurements of nearest shrub and tree at 56 m because of difficulty accurately observing small woody features beyond that range in moderately rolling topography. When no trees or shrubs were present within 56 m, we assigned nearest shrub and tree distances of 99 m. Even though this value was arbitrary, we tested a number of other values between 57–150 m to be sure that the choice of this maximum value did not affect any of our conclusions. We also counted the number of lone trees and shrubs within 56 m of each nest.

We used ArcGIS (version 9.3.1, ESRI, Redlands, CA) to create a digitized land-cover layer based on 2008–2010 aerial images from the National Agriculture Imagery

Program (United States Department of Agriculture). We categorized the landscape as cropland, grassland, woodlot, wetland, or other (including roadways, farmyards, and other developed areas). We used this layer to assess percentage land cover of grass, wetland, and trees at 3 scales: 3.1 ha (100-m radius around nest), 78.5 ha (500-m radius), and site-level (Greenwood et al. 1995, Stephens et al. 2005). We generated site-level data by placing an 800-m buffer around each nest and then dissolving borders to create a single site-level polygon around all nests at a given WPA. Site-level polygons ranged from 236–597 ha depending on area searched and distribution of located nests.

We measured distances from nests to major wetland edges and woodlots using aerial images (Phillips et al 2003). We defined major wetlands as seasonal, semipermanent, or permanent wetlands that were ≥0.4 ha (Cowardin et al. 1979). Woodlots were defined as any woody feature composed of >0.1 ha of closely spaced trees.

Data Analysis

We modeled the logit of daily survival rate (DSR) as a function of nest- and occasion-specific predictor variables using generalized nonlinear mixed models in SAS NLMIXED (SAS Institute Inc., Cary, NC; Rotella et al. 2004, Shaffer 2004). We identified an a priori set of covariates that potentially influenced DSR of nests and proceeded with model selection in 3 stages (Fondell et al. 2008, Amundson and Arnold 2011) using Akaike's information criterion (AIC) to compare and rank models within each stage (Burnham and Anderson 2002).

The first modeling stage included covariates unrelated to habitat: nest age in days, Julian initiation date, species, and a variable combining site and year (Klett and Johnson 1982, Beauchamp et al. 1996, Emery et al. 2005, Arnold et al. 2007). An iterative statement within the NLMIXED model allowed nest age to be incremented by 1 day for each additional exposure day (Rotella et al. 2004). We considered both linear and quadratic terms for initiation date and nest age. Species was coded using dummy variables to distinguish 3 groups: blue-winged teal (*Anas discors*), mallard (*A. platyrhynchos*), and all other species combined: northern shoveler (*A. clypeata*), northern pintail (*A. acuta*), American wigeon (*A. americana*), and gadwall (*A. strepera*). We treated site-year as a normally-distributed random effect on the intercept to account for non-independent fates among nests sampled at the same site during the same year (Rotella et al. 2004). We began modeling with an intercept only and sequentially added a single variable, which was retained if it led to a reduction in AIC.

In the second stage, we added landscape and habitat covariates unrelated to woody vegetation to the best-supported model from stage 1. These included: distance to wetland edge, standardized VOR, percent grass measured at 3 scales, and percent wetland at 3 scales. Because habitat features measured at different spatial scales were strongly correlated (e.g. % wetland at 100 m, 500 m, and site level), we retained the level that was most strongly supported based on smallest AIC. Measurements of VOR were confounded with date, so we included a VOR × initiation date interaction. In the third stage, we used the best-supported model from stage 2 and individually added each of 8 covariates that quantified different aspects of woody vegetation: nearest tree, nearest shrub, number of trees within 56 m, number of shrubs within 56 m, distance to nearest woodlot, percent trees at 100 m, percent trees at 500 m, and percent trees at site level.

We converted estimates of DSR to nest success by raising DSR to the 35th power (Klett et al. 1986). When graphing relationships between nest survival rates and individual covariates, we converted DSR values to nest success by holding other modeled covariates constant at their mean values, except nest age, which we modeled as the product of survival rates from initiation to hatch ($\prod_{i=1}^{35} DSR_{ij}$) where i represents nest age in days and j is the covariate being graphed. We calculated confidence intervals that recognized prediction uncertainty over all modeled variables by using ESTIMATE (fixed effect) and PREDICT (random effect) statements in SAS (Rotella et al. 2004). We used 85% confidence intervals because AIC-based model selection will tend to support the inclusion of variables when 85% confidence intervals do not include zero (Arnold 2010).

2.4 RESULTS

We searched 1,226 ha on 33 WPAs between 2008 and 2010. We located 1,064 duck nests, including 684 (64%) blue-winged teal, 262 (24%) mallard, 61 (6%) gadwall, 38 (4%) northern shoveler, 14 (1%) northern pintail, 1 American wigeon, and 4 unknown. Final fates included 342 successful nests (32%) and 623 (59%) nests destroyed by predation. Nest abandonment was attributed to partial predation (n = 33), investigator disturbance (17), and unknown causes (20). Few nests failed for other reasons, including investigator damage (23), unviable eggs (1), machinery (1), flooding (1), and unknown fates (3). Our sample size for survival analysis included 10,293 exposure intervals (Rotella et al. 2004) from 1,009 nests.

In our best-approximating model from stage 1 (Table 1), DSR was a function of 3 variables: site-year, initiation date, and nest age. After the second stage of modeling, the best-supported model was: logit (DSR_i) = 3.526[SE 0.5958] ± 0.1593[SE 0.0567] × site-year − 0.0110[SE 0.0034] × initiation date + 0.0361[SE 0.0065] × age + 0.9483[SE 0.3588] × percentage of grassland within 500 m − 0.9225[SE 0.3728] × percentage of wetland within 100 m + 2.1934[SE 0.5375] × VOR − 0.0135[SE 0.0035] × VOR × initiation date. Including a random effect for site-year dramatically improved model fit (ΔAIC = 35.7). Nest success ranged from 1.5% (85% CI: 0.5–2.5) to 38.7% (85% CI: 29.9–44.4) among site-years, with replicated sites indicating both spatial and temporal components to this variation (Fig. 1). Daily survival rate was affected by both nest age and initiation date (Fig. 2), increasing from nest day 1 (0.9097; 85% CI: 0.8938–0.9255) to nest day 35 (0.9719; 85% CI: 0.9663–0.9774). Models predicted that overall nest success decreased from 18.0% (85% CI: 13.6–23.8%) for nests initiated on 8 May to 7.2% (85% CI: 5.1–10.3%) for nests initiated on 18 June. More grass in the surrounding 500 m was associated with greater nest success. Predicted nest success ranged from 7.9% (85% CI: 5.32–11.6%) for nests with 25.8% surrounding grass (10th percentile) to 17.4% (85% CI: 13.2–22.9%) for nests with 67.2% surrounding grass (90th percentile; Fig. 3). Amount of wetland within 100 m had a negative effect on nest survival, with predicted nest success averaging 14.5% (85% CI: 11.3–18.7%) for nests with no wetland within 100 m to 8.8% (85% CI: 6.1–12.0%) for nests with 27% wetland within 100 m (90th percentile; Fig 3). Nest success increased strongly with VOR for nests initiated early in the season, but the benefit of high VOR decreased as the season progressed (Fig. 4).

Models with 2008 data omitted had essentially identical beta estimates for VOR and the interaction between VOR and initiation date when compared to models where missing VOR values were replaced with the mean.

In the final stage of modeling, only 1 of 8 woody vegetation covariates led to a smaller AIC score (Table 2); DSR increased with the number of trees within 56 m (Fig. 5). Our best-supported model with woody vegetation predicted 11% nest success for nests without trees in the surrounding 56 m and 14% nest success for those with 2 trees (90th percentile) or 18% for nests with 5 (95th percentile) trees within 56 m. Woody vegetation covariates were not highly correlated with other habitat-related model parameters; the greatest correlation coefficients were 0.15 for percentage of wetland within 100 m and distance to nearest shrub and 0.27 for percentage of grass within 500 m and distance to nearest woodlot.

2.5 DISCUSSION

Encroaching shrubs and trees did not pose a threat to duck nest survival in this study. Only 1 of 8 variables related to tree abundance was supported by a smaller AIC in our analysis, and contrary to our a priori expectations, this model suggested that nests survived better if they were located near scattered trees. By considering 8 individual woody vegetation covariates, we did increase our chances of finding a spurious effect, but number of trees within 1 ha led to a considerable reduction in AIC (−9.3). We have few explanations for why scattered trees might be beneficial for nesting waterfowl. Predators might avoid foraging within regions of scattered trees because scattered trees are an unusual and thus foreign habitat, but given the wide variety of generalist nest predators in the region, this seems unlikely (Sargeant et al. 1993). Smaller nest predators may avoid foraging within sparsely wooded areas because they fear avian predators (e.g. red-tailed hawks), but this should then also hold true for proximity to woodlots.

All of the hypothesized reasons why trees might be detrimental to nesting ducks (e.g., providing necessary or preferred habitat, or altering movement or foraging patterns of certain predators) seemed reasonable and consistent with widely accepted ideas about predator ecology and nest survival (Phillips et al. 2003, Grant et al. 2004, Grant et al. 2006), and we were surprised that we did not find at least a weak negative effect of woody vegetation on nest survival rates. Given the wide array of predators that will eat duck eggs, management activities targeted at any single predator species or group (i.e., woodland predators) may have little effect on overall predation rate given compensatory predation by other species (Greenwood 1986, Greenwood et al. 1998). Active removal of shelterbelts in Wisconsin grasslands caused a shift in the types of nest predators and an increase in breeding density, but no overall change in nest survival rates for grassland songbirds (C. Ribic, USGS Wisconsin Cooperative Wildlife Research Unit, personal communication). Renfrew and Ribic (2003) found that woodland predators traveled up to 200 m into grassland habitat to depredate nests, and tree removal at the level of individual WPAs (median size 63 ha) may be ineffective at altering foraging behavior of local predators.

American crows are a frequent predator of waterfowl nests (Sargeant et al. 1993) and we expected that crows would particularly benefit from the presence of scattered trees, but we did not observe crows on any of our study sites during 2008–2010. Regional crow populations declined dramatically in the wake of West Nile virus and overall populations were at half of normal numbers (LaDeau et al. 2007). Studies may find different outcomes if repeated in areas where crows or other avian predators are more numerous.

Although woody vegetation appeared not to affect nest survival rates, we identified several other variables that influenced nest survival in our study. Our best-supported model included negative effects of nesting near wetlands and positive effects of nesting early in the year, in areas with a high percentage of grass, and in dense vegetation, although this last benefit waned later in the season. Nests located near wetlands were less likely to be successful, a pattern observed in other studies (Krapu et al. 1997, Stephens et al. 2005). We commonly observed skunks (*Mephitis mephitis*) on our study sites and studies of foraging behavior have revealed that skunks are more likely to forage near wetlands margins (Greenwood et al. 1998, Larivière and Messier 2000, Phillips et al. 2003). Although wetlands are essential for attracting breeding pairs and providing brood-rearing habitat (Krapu et al. 2006, Arnold et al. 2007), ducks appear to benefit from nesting >100 m from the nearest wetland.

Duck nesting studies have almost ubiquitously identified a positive effect on nest success from nesting in areas with greater expanses of perennial cover (Greenwood et al. 1995, Garrettson and Rohwer 2001, Reynolds et al. 2001, Stephens et al. 2005; but see Arnold et al. 2007), and our study was no exception. Even in a highly cultivated landscape and on sites that were often quite small, nests with more extensive grass in the surrounding 0.5 km provided the greatest nest survival rates.

We noted a linear decline in nest success throughout the breeding season (Emery et al. 2005, Arnold et al. 2007), but other studies have noted seasonal increases (Greenwood et al. 1995, Garrettson and Rohwer 2001) or non-linear patterns (Emery et al. 2005, Pieron and Rohwer 2010) in nest success throughout the nesting season. Seasonal trends in nest survival rates likely reflect changes in predator foraging in response to increasing vegetation cover, increasing density of nesting birds, or changing availability of alternate prey or food sources (Grant et al. 2005). Because early-initiated nests are particularly influential for recruitment (Dzus and Clark 1998), efforts to provide high quality habitat to early-nesting ducks may be especially beneficial (Emery et al. 2005).

Visual obstruction was an influential predictor of nest success, particularly for nests initiated early in the season. Nest concealment is more likely to be crucial when avian predators are dominant (Clark and Nudds 1991). Early-nesting ducks that were able to locate dense, tall residual cover or early-season grasses had a strong advantage, even though we suspect skunks and raccoons were the most common nest predators on our sites. As cover density increased throughout the nesting season, the advantage of nesting in thick cover dissipated.

Although we measured habitat variables at multiple scales (i.e., 56-m, 100-m, and 500-m radii around nests; 800-m radii around all nests in aggregate), models did not support any of the 800-m covariates (e.g., % trees, % grass, or % wetland). This is encouraging information for waterfowl managers who are hampered by small land holdings, since it suggests that management efforts at smaller scales (i.e., quarter-sections) may still provide benefits to nesting waterfowl.

2.6 MANAGEMENT IMPLICATIONS

Our study indicated that tree-removal would be ineffective for increasing waterfowl nest success. Effective long-term management of grasslands for nesting cover requires periodic burning, mowing, or grazing to maintain desirable vegetative characteristics (Devries and Armstrong 2011), and such activities (especially burning and haying) help to prevent encroachment of woody vegetation into grassland habitat. For grasslands where waterfowl nest success is a primary management objective, we recommend that managers focus their attention on adding grassland and maintaining vigorous stands of nesting cover, while managing against woody vegetation only to the extent that it threatens the persistence and health of grassland plant communities. Our results suggest that scattered trees and woodlots pose little risk to nesting waterfowl.

Table 1. Model selection results from analysis of waterfowl nest success in west-central Minnesota, USA, 2008–2010. Potential stage 1 variables included intercept, random effect of site-by-year (SITE-YEAR), species (SPECIES), Julian initiation date (INIT, $INIT^2$), and nest age (AGE, AGE^2). Potential stage 2 variables included visual obstruction reading (VOR) and percent wetland (WET) and grass (GRASS) measured at 3 nested scales: 100m, 500m, and site (mean = 415 ha). Models were ranked according to differences in Akaike's information criteria (ΔAIC) and ΔAIC values and model weights are shown separately for each stage.

	Model	Parameters	Δ AIC	Model weight
Stage 1	Intercept + SITE-YEAR + INIT + AGE [a]	4	0.0	1.0000
	Intercept + SITE-YEAR + INIT	3	62.5	0.0000
	Intercept + SITE-YEAR	2	90.0	0.0000
	Intercept	1	125.7	0.0000
Stage 2	Stage 1 + $GRASS_{500}$ + WET_{100} + VOR + VOR×INIT	8	0.0	0.9976
	Stage 1 + $GRASS_{500}$ + WET_{100} + VOR	7	12.3	0.0021
	Stage 1 + $GRASS_{500}$ + WET_{100}	6	16.4	0.0003
	Stage 1+ $GRASS_{500}$	5	20.1	0.0000

[a] AIC-best model from stage 1 (AIC = 2,101.4) continued on to stage 2, and AIC-best model from stage 2 (AIC = 2,070.5) was used to test for effects of woody vegetation.

Table 2. Models assessing effects of woody vegetation on waterfowl nest survival rates from 44 site-years in Minnesota, USA 2008–2010. Each individual measure of woody vegetation extent or proximity was added to the best model from stage 2 (site-year + initiation date + age + percentage of grassland within 500 m + percentage of wetland within 100 m + visual obstruction reading (VOR) + VOR × initiation date).

Woody vegetation covariate	ΔAIC [a]	β	SE(β)
Sum of lone trees within 56 m	−9.3	0.0533	0.0196
Nearest woody feature >15 trees	2.4	−0.0002	0.0002
% trees within 100 m	2.5	1.6252	1.5103
Distance to nearest lone tree	2.6	−0.0017	0.0016
% trees within 800 m	2.8	−4.0833	3.9910
Distance to nearest shrub	3.5	0.0007	0.0012
Sum of shrubs within 56 m	3.7	0.0011	0.0029
% trees within 500m	3.8	0.0567	2.2246

[a] best model from stage 2 had AIC of 2,068.7.

Figure 1. Model-based estimates of waterfowl nest success and 85% confidence intervals for multiple years and study sites in west-central Minnesota, USA, 2008–2010 illustrating

the prominence of both site and year effects. Sites surveyed in 2008 appear in black, 2009 in white, and 2010 are striped. Estimates are based on a 35-day exposure period and the best model for nest success before accounting for effects of woody vegetation.

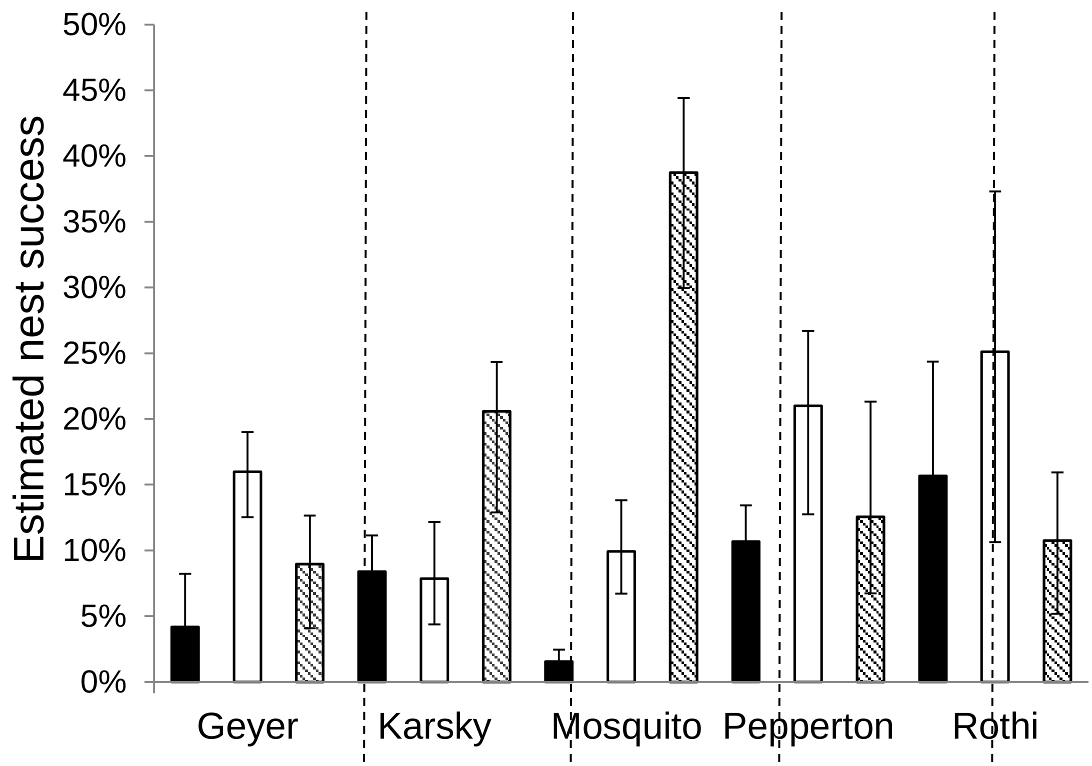


Figure 2. Model-derived estimates of daily nest survival from day 0 to day 35 for representative nest initiation dates in Minnesota, USA, 2008–2010. We derived estimates from the best approximating model before accounting for effects of woody vegetation. Covariates other than initiation date and nest age were held at average values: proportion grass (0.466), proportion wetland (0.098), visual obstruction reading (VOR; 3.08), VOR (3.08) × initiation date. Initiation dates represent 10th percentile (8 May, solid line) and 90th percentile (18 June, dashed line).

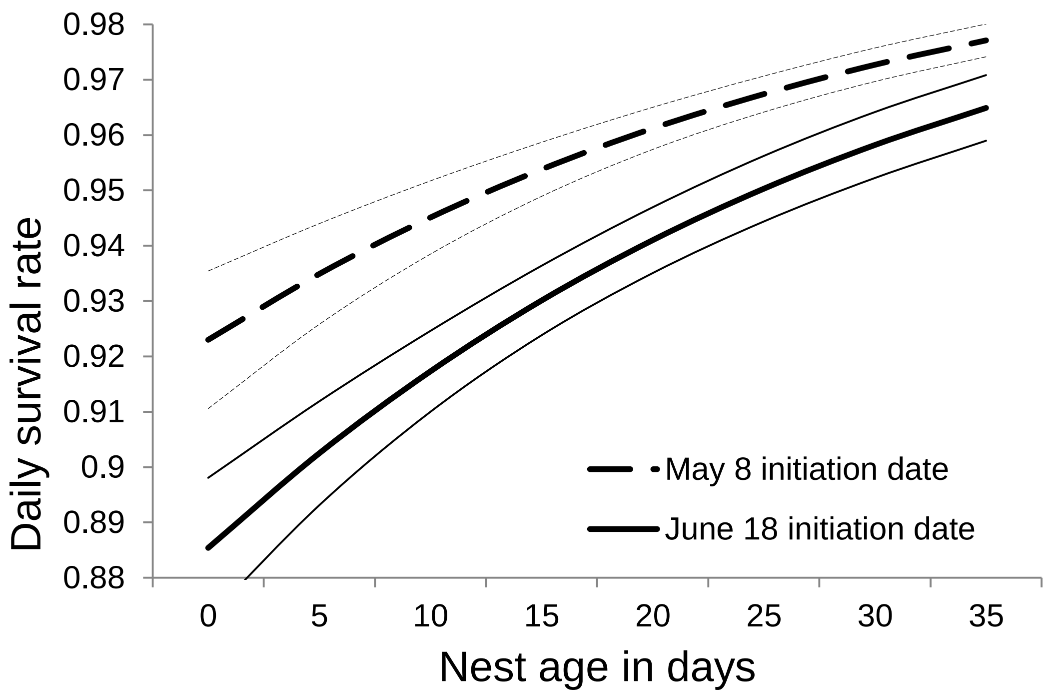


Figure 3. Estimates of waterfowl nest success (± 85% CI) in relation to percent grass within 500 m at 2 values of wetland area within 100 m. We derived estimates from the daily survival rate (DSR) of the best-approximating model before accounting for effects of woody vegetation for sites in west-central Minnesota, USA, 2008–2010. Covariate values for percent grass range from 10–90th percentile, whereas wetland values represent the 10th (0%) and 90th (26%) percentile. All other covariates were held constant at their average values: ordinal initiation date (146.6), nest age (14 days), visual obstruction reading (VOR; 3.08), and VOR (3.08) × initiation date (146.6).

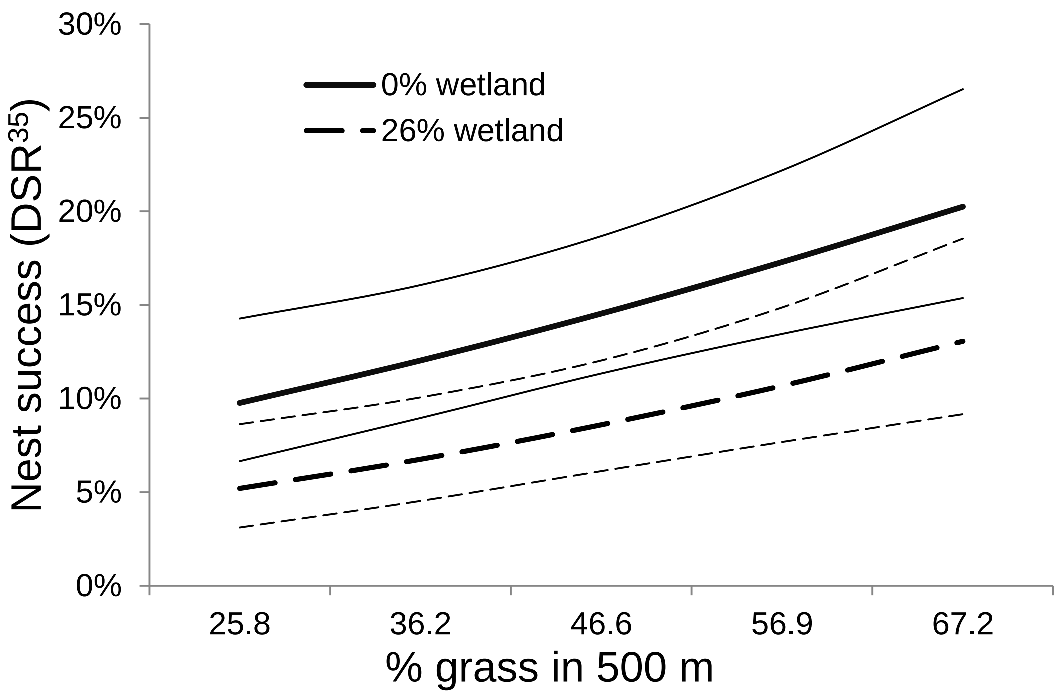


Figure 4. Estimates of nest success (± 85% CI) relative to visual obstruction reading (VOR) and nest initiation date, derived from the daily survival rate (DSR) of the best-approximating model before accounting for effects of woody vegetation for duck nests in west-central Minnesota, 2008–2010. Covariate values for initiation date represent 10–90th percentile, VOR represent average (2.5 dm) and 90th percentile (5.0 dm) and all other covariates were held constant at average values: nest age (14 days), proportion grass (0.466), and proportion wetland (0.098).

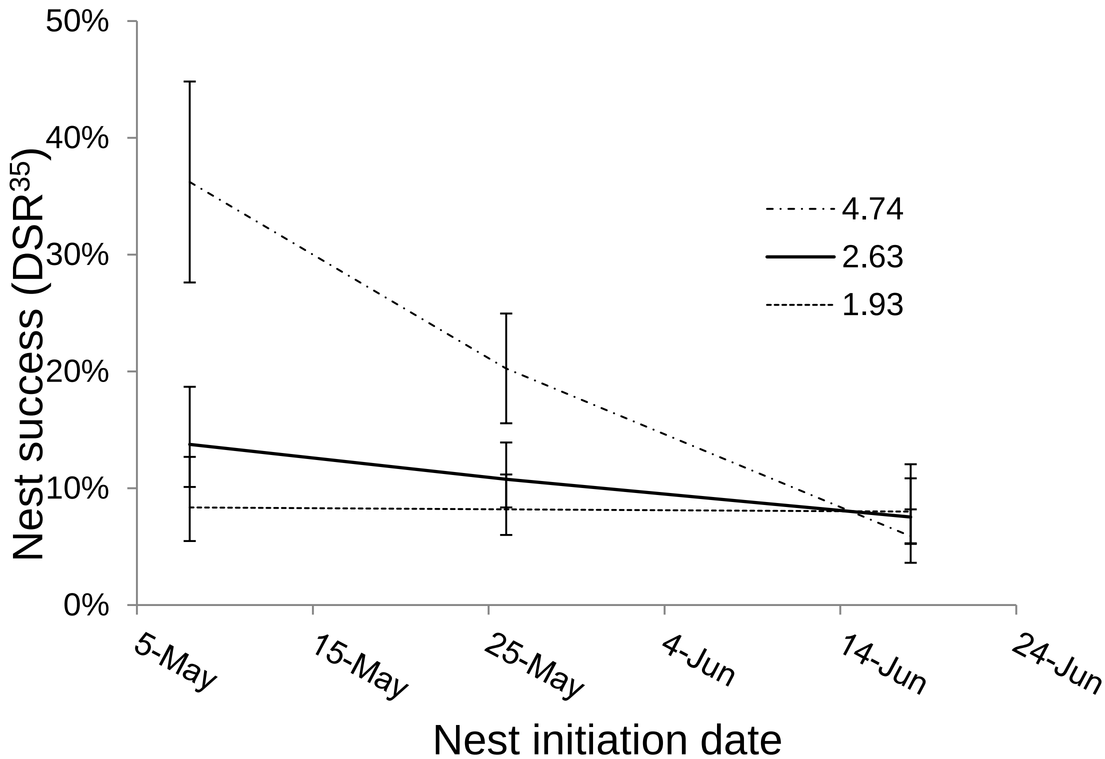
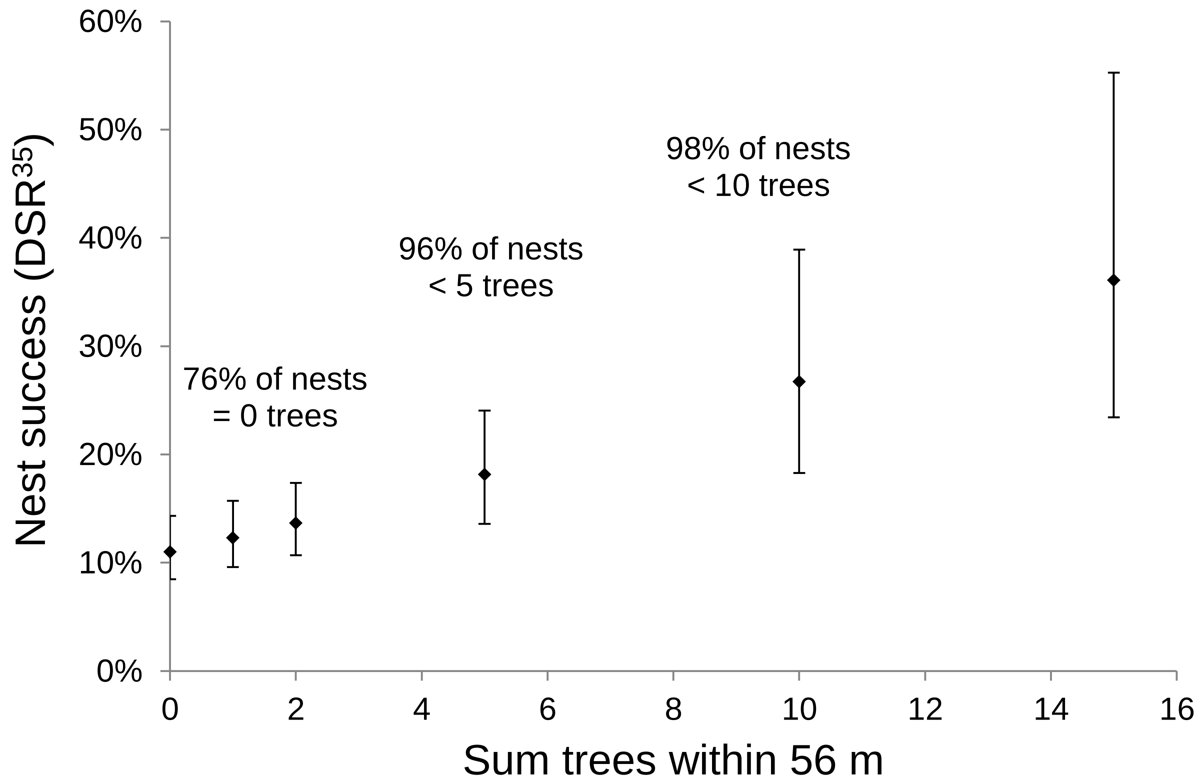


Figure 5. The lines represent estimates of waterfowl nest success (± 85% CI) relative to number of trees within a 1-ha circle surrounding the nest. Estimates are based on the daily survival rate (DSR) of the best-approximating model for sites in west-central Minnesota, USA, 2008–2010. The histogram corresponds to the right axis and shows the percent of 1,009 nests with 0–15 trees in the surrounding 1-ha circle. All covariates other than trees were held constant at average values: ordinal initiation date (146.6), nest age (14 days), proportion grass (0.466) proportion wetland (0.098), visual obstruction reading (VOR; 3.08), and VOR (3.08) × initiation date (146.6).



CHAPTER 3

GRASSLAND BIRDS DEMONSTRATE DELAYED RESPONSE TO EXPERIMENTAL TREE-REMOVAL

3.1 INTRODUCTION

North American grassland birds are experiencing widespread declines (Igl and Johnson 1997, Sauer and Peterjohn 1999, Sauer et al. 2012). These declines are likely due to extensive loss of habitat (Knopf and Samson 1997), but degradation of existing habitat also affects the productivity of breeding grassland birds (Lloyd and Martin 2005, Mineau and Whiteside 2013). A key element of habitat degradation in grasslands is a lack of frequent disturbance (e.g., fire, grazing) on small, isolated remnant grasslands patches. This lack of disturbance, combined with intentional planting of trees and shrubs by humans, has culminated in the expansion of woody vegetation onto grassland systems around the world (Grover and Musick 1990, Archer et al. 1994, Jackson et al. 2002, Huxman et al. 2005). In many regions, acquiring new land for restoration into grassland habitat is fiscally or logistically infeasible and therefore conservation efforts have increasingly focused on improving existing grasslands with treatments such as tree-removal (USFWS 2003).

Research has consistently demonstrated that the presence of woody vegetation negatively influences abundance or presence for most species of native grassland birds (Fletcher et al. 2003, Winter et al. 2006, Quamen 2007, Thompson 2013: chapter 1) and that these negative impacts can stretch far from the edges of a woodlot or shelterbelt (Cunningham and Johnson 2006, Thogmartin et al. 2006, Renfrew and Ribic 2008). Typical woodlots rarely provide important habitat for woodland-associated avian species of concern (Kelsey et al. 2006). Trees or wooded edges have been associated with reduced survival of ring-necked pheasants *Phasianus colchicus* (Schmitz and Clark 1999) reduced nest success of waterfowl (Gazda et al. 2002) and reduced habitat suitability and population declines of prairie grouse (Niemuth 2003).

There are numerous underlying mechanisms by which woody vegetation may detrimentally affect grassland birds. For example, the presence of trees may provide novel habitat niches that attract generalist avian species and increase competition for resources (Kelsey et al. 2006). Trees host numerous predator species that are otherwise uncommon on grasslands and are thought to lead to increased predation pressure on grassland birds and nests (Sargeant et al. 1993). The presence of high vantage points offered by trees or shrubs is thought to increase risk of nest predation by avian predators and nest parasitism by brown-headed cowbirds *Molothrus ater* (Johnson and Temple 1990). Finally, grassland birds may possess an innate avoidance of tall or foreign features that is of little current consequence to fitness (Renfrew et al. 2005). Without experimental studies, we lack the ability to determine if woody vegetation is the key feature underlying these observed detrimental effects. For example, woody vegetation encroachment may be more likely to occur on grassland sites are already degraded in other ways (e.g. insufficient burning or grazing treatments) such that tree-removal alone may not lead to increased grassland bird abundance.

An experimental removal of trees is necessary in order to demonstrate that trees are the primary cause of reduced grassland bird abundance, not other potentially correlated habitat variables. To date, the only such experiments have been relatively small in scale, focusing on removal of linear features (single tree-rows or shelterbelts;

Quamen 2007, Ellison et al. 2013). Our study differs in that it represents a large-scale study, over a longer time period, wherein large woodlots, shelterbelts, and scattered trees were removed with the intention of rehabilitating six large grassland areas (771 ha total). Techniques used to remove trees were representative of those employed by land managers and thus we expect responses in our study to be reflective of those managers can expect, given commonly utilized tree-removal practices. Our primary objective was to examine the impact of tree-removal treatment on bird abundance with a focus on grassland birds. Our secondary objective was to examine efficacy of large-scale tree and shrub removal treatments to reduce woody vegetation, particularly over the seven-year duration of our study. We predicted that tree-removal would be beneficial for ground-nesting grassland birds, negative for birds that nest in cavities or mature trees and neutral for birds that nest in wetlands.

3.2 MATERIALS AND METHODS

Study sites

All study sites were federally-owned and managed grasslands (i.e. U.S. Fish and Wildlife Service Waterfowl Production Areas) located throughout a 120 × 65 km region in west-central Minnesota (Fig. 1). Sites ranged from 75-280 ha ($\bar{x}$ = 145 ha). Treatment sites were previously identified by managers as priority sites for habitat improvement. Control sites were then selected such that each control matched a treatment site as closely as possible in location, size, quality, and extent of woody vegetation.

Grass and forb composition varied widely within and between sites, but most sites were reconstructed grasslands (converted from agricultural use back to perennial grass cover). All study sites were Waterfowl Production Areas, and thus the primary purpose of these grasslands was to conserve or create wetland and upland habitat for waterfowl, not necessarily to provide high-quality native grassland habitat. Tree species targeted for removal commonly included eastern cottonwood *Populus deltoides*, eastern red-cedar *Juniperus virginiana*, box elder *Acer negundo*, and green ash *Fraxinus pennsylvanica*. Shrub species targeted for removal included non-native species (e.g. Russian olive *Elaeagnus angustifolia* and buckthorn *Rhamnus cathartica*) as well as native species that had become excessively abundant (e.g. wild plum *Prunus americana*, sandbar willow *Salix interior*).

Experimental design

We used a modified Before-After–Control-Impact experimental design (Stewart-Oaten et al. 1986). The study began in 2005 with six control and six treatment sites. Two more control sites were added in 2007 and two of the original control sites were eventually treated in 2008 (Figure 1, Table 1). In order to maintain synchronicity of treatments (all occurring in the winter of 2005-2006), we omitted data collected on these two control sites after late treatments (2007-2008; Table 1). Initial surveys were conducted in 2005 and in the following fall and winter contractors were hired to remove woody vegetation from six treatment sites. Methods for tree-removal varied depending on the density and size (diameter at breast height or dbh) of woody vegetation. Contractors removed shrubs and small trees (dbh 10.2 − 40.6 cm) using skid-steers outfitted with appropriate cutting tools (shear, timber-ax, or carbide saw attachments). When dbh exceeded 40.6 cm, trees were felled by hand with chainsaws. After cutting, stumps were treated with herbicide to prevent suckering (Garlon 4 ™ with solution strength of 20-

25%, mixed with Bark-Oil-Blue). Cut woody vegetation was piled, left to dry for approximately two years and then burned. In order to minimize disturbance to surrounding vegetation, tree-removal took place in the fall and winter months while plants were dormant and the ground was frozen. To minimize compaction of soil, all skid-steers had rubber tracks rather than tires. The estimated cost of paying contractors, maintaining and repairing equipment, fuel, herbicide, and staff hours for a tree-removal, on average, was $40,000 USD per site for the initial two years of treatment. The total extent of tree-removal ranged from 4.1 to 28.3 hectares ($\bar{x}$ = 12.2 ha) per site or 4 to 21% of the total site area.

Bird surveys

We arranged point count stations on each site starting with a random point and then placing the other points in a rectangular grid pattern, 150 m apart. If more than 20 points fit within the site, 20 were chosen randomly. We conducted a single point count annually at each station, between 2 June and 4 July. Bird surveys were conducted between sunrise and noon on days without strong winds (< 25 km/hr) or steady precipitation. For the purposes of this study, we omitted birds noted as fly-overs and those recorded beyond 100 m from the observer. Because count circles overlapped, observers also noted if any birds were likely repeats (i.e. a meadowlark singing from the same perch during 2 different point counts) and birds marked as potential repeats were omitted from analysis.

Herbaceous cover and woody vegetation surveys:

We recorded litter depth at 5, 10, 15, 20 and 25 m from the center of a point count circle by placing a ruler into dead plant debris and recording the litter height to the nearest 0.5 cm above soil (SRM Task Group 1995). We combined these five measurements to generate an average annual litter depth measurement. We took grass height and density measurements by placing a pole at the center of the point count circle and recording visual obstruction to the nearest 0.5 dm from 4 m away at 1 m viewing height in each cardinal direction (Robel et al. 1970). We assessed average distance to trees, shrubs, and slash piles (measurements to slash piles started in 2006) by using laser rangefinders to measure the distance to each feature in each of four quadrats (NE, SE, NW, and SW). We differentiated between trees and shrubs by height (< 6-m, shrub; > 6-m, tree) and growth form (trees single stemmed, shrubs often multi-stemmed).

Data Analysis

Preliminary assessment of bird detection rates did not uncover any troublesome issues (methods following Chapter 2). Most importantly, variation in detection should not be confounded with trees or tree-removal treatments and we found no evidence for this. The only variable that consistently influenced detection was observer. Considering the duration of the study, we had a very small number of observers (n = 6), with a single observer often conducting all surveys on a site in all years. We found no major shifts in observers, and in particular, no major changes that corresponded with the timing of treatment on any single site. Because our surveys were conducted in clusters and repeatedly over time, the inclusion of a random term for site was critical to avoid pseudo-replication (Hurlbert 1984). We thus determined that it was appropriate to proceed with a modeling approach that allowed the inclusion of random effects and did not explicitly model variation in detection.

In reviewing the statistical methods used in similar unbalanced, ecological-scale BACI studies, we found a variety of analyses were employed (Hanowski et al. 2003, Haché and Villard 2010, Chizinski et al. 2011, Holmes et al. 2012). None of these studies explicitly modeled detection, all used generalized mixed models, and focused on the significance of the interaction of time and treatment. Given our non-random selection of treatment sites, the extended time-period of "treatments", unbalanced study design, and the variation in potential response to treatment, we determined selected a small group of potential models that exemplified different potential responses to treatment.

We examined vegetation and avian response to treatment using generalized linear mixed models (GLMMs) with the *lme4* package in R (Bates et al. 2013), R Development Core Team, 2013), and following recommendations in Bolker *et al.* (2009). Because we were primarily interested in assessing response to treatments, we considered five models that each represented different potential responses to treatment (Table 2, Fig. 2). Our null model included an intercept (mean abundance) and a random site effect (i.e. abundance varied by site), which was appropriate given the replication of counts within sites. A random effect of site is also appropriate as we were interested in making inference about all similar sites in the region, not just our sample. The first model included fixed year effects for situations where bird populations varied annually, but not in relation to treatment (year-only). The remaining models examined 3 potential treatment responses: 1) a singular response to treatment without annual variation (trt.i, not to be confused with treatment-only effects, trt.i is an indicator variable for treated or not treated where all control sites are coded 0 and treated sites are 0 until treated), 2) a singular response to treatment with annual variation that was consistent over years (trt.i + yr), and 3) an interaction of year and treatment such that treatment responses differed from control and displayed annual variation in that response (trt × yr). All models were fit using a Poisson distribution (log link) and Laplace approximation and we used Akaike information criterion to select the best approximating model from our set of 5 models (Burnham and Anderson 2002, Bolker et al. 2009).

We assumed that there was no evidence of a treatment response when the null or year-only models were better supported than the other three models including treatment effects. When the interaction model was supported, we focused interpretation on the resulting interactive terms, assessing significance when z-tests for specific year-treatment interaction coefficients resulted in $p \leq 0.05$ (Zuur *et al.* 2009). We generated plots of bird abundance using model estimates from the trt × yr model with 85% confidence intervals (Arnold 2010); plots ignore variation due to random site effects and represent predicted abundance at a site with geometric mean abundance. We used a similar approach for analyzing the response of vegetation measurements to treatment, but used Gaussian error distributions given variables were measured on a continuous scale.

3.3 RESULTS

During 2005-2011, we conducted 1,756 point count and vegetation surveys on 14 sites. We detected 18,969 individual birds of 114 species, but only 2,733 of these were grassland birds (Table 4). Many of the more commonly observed species were wetland-associated or generalist species like red-winged blackbirds *Agelaius phoeniceus* (n = 3,996), common yellowthroats *Geothlypis trichas* (n = 1,688) and song sparrows *Melospiza melodia* (n = 1,173). The most common grassland-obligate birds were clay-colored sparrows *Spizella pallida* (n = 1,332), bobolinks *Dolichonyx oryzivorus* (n = 708), and sedge wrens *Cistothorus platensis* (n = 589); with other grassland species accounting for 0.05% of detections (Table 4). We examined the responses of the 15 most commonly observed species plus willow flycatchers *Empidonax traillii* (ranked 20th in abundance, but a species of regional conservation concern; n = 199). We then combined less-commonly observed species into groups based on nest-site location and general habitat preferences (e.g., cavity nest-woodland, tree/shrub nest-woodland, tree/shrub nest-general, ground nest-wetland, floating nest-wetland, ground nest-grassland; Ehrlich et al. 1988; Table 4). Additionally, we examined the response of waterfowl (Anseriformes) and all grassland birds combined (including those modeled individually, as a group, or omitted elsewhere), because these groups were both management priorities. Species that did not readily fit into one of these categories were omitted.

Vegetation

Treatment was effective in altering the vegetative community of study sites. All measures of vegetation response were best described by the trt × yr model. On treatment sites, the predicted distance to trees increased from 79 m (95% prediction interval: 15.2 - 142.0) in 2005 to 576 m (512.6 - 639.5) in 2006 and remained considerably higher than at control sites for all subsequent years (Fig. 3A). Average distance to shrub also increased significantly on treated sites, but returned to pre-treatment levels in later years of the study (Fig. 3B). Slash piles appeared on treated sites in 2006 and remnant piles were still present at the conclusion of the study (Fig. 3C). Although not intentionally manipulated, litter depth on treated sites decreased between 2005 and 2007 from 5.71 to 1.38 (Fig. 3D). The trt × yr model was also best supported for grass height and density. Only one treatment by year combination was significant with control sites in year 5 having comparatively higher and denser grass (Fig. 3E).

Grassland birds

On control sites, model-estimated abundance of total grassland birds in year 0 was 1.98 (geometric mean; SE: 0.23) per 100 m radius count area and counts steadily declined to 0.76 (SE: 0.09) by year 2011. On treated sites, average abundance decreased from 2.06 (SE: 0.19) in year 0 to a low of 0.90 (SE: 0.10) in year 2, but then increased in subsequent years with the yr × trt model supporting a positive treatment effect in years 4, 5, and 6 (Fig 4D, Table 5). We observed a small number of other grassland birds (n = 97) and this group was best described by trt.i + yr (Fig. 4E).

The best-approximating model for all individual grassland bird species was trt × y, the full interaction of time and treatment. Bobolink *D. oryzivorus* decreased significantly on treatment sites in year 2, but rebounded in year 3 and abundance remained similar to control sites for the remainder of the study (Fig. 5C). Clay-colored sparrow *S. pallida* abundance declined significantly on treatment sites in the third year after treatment, but recovered to a significant positive treatment effect for years 5 and 6 (Fig. 5D). Sedge wren *C. platensis* also decreased significantly in year 2 on treatment sites, but reversed the trend and by year 5, treatment was significantly positive (Fig. 5H).

Non-grassland birds

The response of three wetland-associated species groups was best approximated by the trt × yr model (waterfowl, wetland-floating nest, wetland-ground nest). We observed consistent positive effects of treatment (study years 2-6) for ground-nesting wetland birds (Fig 4A). Wetland birds with floating nests had a significant, positive response in years 3 and 5 (Fig. 4B) and waterfowl abundance responded positively to treatment during all post-treatment years (Fig. 4C).

Birds that typically use woodland habitat and nest in tree-cavities responded immediately and negatively to treatment without sign of recovery (Fig. 5F). The most parsimonious model for cavity-nesting woodland birds was trt.i + yr (Table 3), indicating that response to treatment occurred quickly and that annual differences in abundance between treatment and control sites were consistent after the treatment occurred. The responses of woodland and general-habitat birds that nest in trees or shrubs were best approximated by trt.i, suggesting a reduction immediately after tree-removal treatment that remained consistent for the duration of the study and demonstrated little annual variation (Fig. 4G & H, Table 3).

Individual species showed greater variation in response with trt × yr selected as the best-approximating model for the majority of individual species (10 of 16; Fig. 5). For several species, the null or year-only model provided the best fit, indicating little impact of treatment or sample sizes that were inadequate to discern impact (Table 3). Species unaffected by treatment were the common yellowthroat *G. trichas*, marsh wren *Cistothorus palustris*, song sparrow *M. melodia*, swamp sparrow *Melospiza georgiana*, tree swallow *Tachycineta bicolor*, and willow flycatcher *Empidonax traillii*.

For species that demonstrated significant interaction of year and treatment, brown-headed cowbirds *M. ater*, and yellow warblers *Setophaga petechia* both showed delayed negative treatment effects that began in years 4 and 3 respectively (Fig. 5B and J). American goldfinches *Spinus tristis* were negatively affected by treatment in 5 of 6 post-treatment years, common grackles *Quiscalus quisculain* in 2 of 6 years and eastern kingbirds *Tyrannus tyrannus* in 1 of 6 years (Fig. 5A, E and F). Red-winged blackbirds *Agelaius phoeniceus* had several interaction terms that were nearly significant ($p < 0.10$), but no individual years-treatment combinations were ultimately supported. Yellow-headed blackbirds *Xanthocephalus xanthocephalus* were positively affected by treatment in 4 of 6 post-treatment years (Fig. 5G).

3.4 DISCUSSION

Vegetation

Tree-removal treatments were successful at reducing the abundance of trees on treatment sites, but they were less successful at controlling shrubs (Fig. 3A and B). Treatments also led to an increase in slash on treated sites. Although efforts were made to burn these piles within the first two years after treatment, slash piles remained for the duration of the study (Fig 3C). Although tree-removal treatments were planned with the intention of reducing additional, unwanted changes to the treated sites (e.g. soil compaction or damage to sod layer), subsequent prescribed fire treatments to control woody vegetation regrowth on treated sites caused notable differences between treatment and control sites (Fig. 3D). In the three years after tree-removal (2006-2008), prescribed fire treatments took place at only one of eight control sites whereas all treatment sites were burned at least once in that same three-year time period (Table 1). Although the purpose of the prescribed fire was to inhibit tree and shrub re-growth, it also led to a temporary reduction in above-ground dead litter on treated sites. Conversely, measurements of grass height and density did not differ between treatment and control sites, even though one would expect fall or spring burn treatments to reduce residual grass height, particularly early in the spring when birds are selecting territories. Most of our vegetation surveys took place after the completion of point count surveys (range: 25

June to 31 August, $\bar{x}$ = 23 July), which may have masked potential early-season differences in grass height and density resulting from prescribed burning on treatment sites. Thus birds that prefer grassland habitat with more residual litter and standing dead grass may have avoided treatment sites for the first few years following tree-removal.

Grassland birds

Grassland birds were the focus of our study and the tree-removal treatment was specifically intended to improve habitat quality for these species. We were surprised to regularly encounter only three grassland bird species on our study sites; many of our study sites represent some of the largest remaining grasslands in the region. Given the weight of evidence indicating that trees adversely affect grassland birds more than any other habitat variable (Cunningham and Johnson 2011; Thompson 2013, chapter 1), we had expected a strong positive response from grassland birds once trees were removed. We were surprised to observe significant negative response to treatment from grouped grassland birds, bobolinks *D. oryzivorus*, and sedge wrens *C. platensis* in year 2, and clay-colored sparrows *S. pallida* in year 3. However, these immediate declines might be a consequence of prescribed fire treatments in the years immediately post-treatment. All three of the most commonly observed grassland species prefer at least moderate amounts of litter and moderately tall vegetation at nest sites (Sample and Mossman 1997), and are known to avoid grasslands after prescribed fire treatments and generally return to normal or peak densities 1-8 years after burning (Knopf and Samson 1997). We did see a significant, positive response in the later years of the study from grouped grassland birds (years 4, 5, and 6), sedge wrens *C. platensis* (year 5), and clay-colored sparrows *S. pallida* (year 5 and 6). These positive responses correspond closely with the recovery of litter depth in year 6 (Fig 3D) and general abatement of burning and other treatments to control woody vegetation regrowth (Table 1). For clay-colored sparrows *S. pallida*, the recovery in year 5 and 6 likely also relates to regrowth of shrubs as this species is known to commonly nest in shrubs and tends to prefer habitat with low woody vegetation (Arnold and Higgins 1986).

Numerous grassland bird species prefer to nest on grasslands with sparse vegetation and limited litter (e.g. upland sandpiper *Bartramia longicauda* and grasshopper sparrow *Ammodramus savannarum;* Knopf and Samson 1997) and it is reasonable to expect those species to utilize our treated sites in the 1-3 years after tree-removal. However, these species were uncommon in our study sites and rare in the surrounding region. Although numbers are small, results do tentatively indicated that some of these rare species preferred treated sites. In the six years after treatment (2006-2011), 8 grasshopper sparrows *A. savannarum* were observed on treated sites and only 1 on control sites; 4 upland sandpipers *B. longicauda*, were seen on treated sites and 3 on control. Savannah sparrows *Passerculus sandwichensis* were surprisingly uncommon on our sites; we observed 11 on control sites and 20 on treated sites in post-treatment years. The low abundance and variety of grassland birds may have further contributed to the slow response to treatment because of a lack of birds available to colonize treated sites.

In two similar studies, Quamen (2007) and Ellison et al. (2013) reported clear benefits from tree-removal, occurring almost immediately after tree-removal treatments. Both of these studies differed from ours in that they focused on discrete linear tree-rows and grassland habitat immediately adjacent to target woody features. Because the impact of woody vegetation can extend for many meters beyond the edge of the feature, focusing tree-removal efforts on linear tree-rows with a high edge to interior ratio may also serve to maximize the positive impact of removal and minimize recovery time (Thogmartin et al. 2006, Renfrew and Ribic 2008). Thompson (2013: chapter 1) found that grassland bird abundance might be impacted by trees more than 500 m away. Given the average size of our study sites (147 ha, or an area approximately 1200 × 1299 m), if all four sides were surrounded by trees, essentially only a tiny fragment of the interior (3%) would be more than 500 m from these wooded edges. Thus, careful site selection may be important to maximize the benefit of tree-removal treatments, and particularly focusing removal on relatively isolated linear tree-rows may be particularly effective.

Further, Ellison et al. (2013) compared tree-edge versus interior grassland densities collected via intensive spot mapping and Quamen (2007) used transects at varying distances from tree-rows. Our method of gridded point counts, covering most of a site may have been less effective at noting fine-scale changes as it was more likely to include areas far from treatments as well as wetland or open water. However, the goal of our study was to improve the entire grassland site, and our methods reflected these goals.

For managers hoping to conduct similar habitat improvements for grassland birds, it is important to note that positive response may take many years, depending on the method of treatment and type or extent of woody vegetation being removed. If surveys are to be conducted to assess the efficacy of treatment, we recommend planning to conduct surveys for at least 4-5 years post-treatment or, alternatively, conducting surveys every other year. To maximize benefit, managers may want to focus efforts on linear woody features and also on sites with little woody vegetation on external, surrounding lands.

Non-grassland birds

In many situations, it is important that habitat improvement efforts for a group of target species do not have unintended negative consequences for other priority species. We encountered numerous wetland and water birds that are listed as regional species of conservation concern (Minnesota Department of Natural Resources 2006) and all of our sites are managed for the benefit of breeding waterfowl (USFWS 2003). Three species groups were associated with wetlands: wetland, ground nest; wetland, floating nest, and waterfowl. For these three groups, all significant treatment by year interactions were positive (13 of 18 instances, Table 5). In particular, waterfowl demonstrated consistent, positive response to treatment for all post-treatment years. Thus, we can conclude that tree-removal efforts did not adversely affect these groups of species and potentially provided unexpected benefits. Since these areas are purchased with duck-stamp dollars, habitat alterations for other species of concern must not come at the expense of waterfowl and we saw no evidence of such detriments.

It is somewhat perplexing that waterfowl would benefit from tree-removal and associated prescribed fire treatments, given initial negative response of grassland birds. The vast majority of waterfowl observed in counts consisted of mallards *Anas platyrhynchos* and blue-winged teal *Anas discors* (n = 232 and 211 respectively, waterfowl combined = 715). Both species commonly nest in upland grass and tend to avoid recently burned grasslands with little residual grass and litter cover (Livezey 1981). Further, the waterfowl group included 2 cavity nesting species (wood duck *Aix sponsa*, n = 146; and hooded merganser *Lophodytes cucullatus* n = 18), which presumably would also decline after the removal of woody vegetation. It is possible that counts increased not because of higher nest density, but because more mallard *A. platyrhynchos* and blue-winged teal *A. discors* were selecting wetlands on treated sites for foraging or brood-rearing habitat; there is some evidence suggesting that these species avoid ponds with wooded edges for brood-rearing habitat, likely to avoid potential avian predators (Rumble and Flake 1983).

We saw positive or neutral response to treatment from most other wetland birds, and these associations are generally supported by existing research. Black terns *Chlidonias niger*, American coots *Fulica americana*, and eared grebes *Podiceps nigricollis* were negatively associated with woody vegetation in South Dakota, USA (Naugle et al. 1999) and these species made up 49% of our wetland birds with floating nests. The same study found that marsh wrens *C. palustris* and swamp sparrows *M. georgiana* were positively associated with woody vegetation, but we found no response from either species as a result of tree-removal.

Of more than 40 woodland and generalist species encountered, only 6 represented species of conservation concern that breed regionally, confirming the findings of other researchers that planted woodlots and invading trees in grasslands are of limited value as habitat for rare or declining woodland species (Bakker and Higgins 2003, Kelsey et al. 2006, Minnesota Department of Natural Resources 2006). Unsurprisingly, most tree and shrub nesting species that use woodland habitats declined immediately and significantly to treatment and were better described by models that did not allow annual variation in response.

We also found that brown-headed cowbirds *M. ater* responded negatively to tree-removal treatments. This was unexpected given the evidence that they do not require woody vegetation and that they were historically residents of open grasslands (Mayfield 1965, Johnson & Temple 1990). Brown-headed cowbirds often prefer habitat with perches that are above the height of surrounding vegetation (Johnson and Temple 1990). Because our tree-removal treatment created piles of dead woody vegetation and did not consistently remove shrubs, reduced perch availability is unlikely to be the cause of decline. Declines may be due to a reduction in preferred avian hosts, such as yellow warblers *S. petechial*. Cowbird abundance was also significantly higher on treatment sites than control sites in the pre-treatment year (mean of 0.17 (SE =0.05) pre-count on control sites and 0.50 (SE = 0.08) per count on treatment sites 2-sided t-test $p < 0.001$). Thus treatment sites may have been different from control sites in some habitat characteristic before the onset of the study.

Overall, tree-removal treatments were successful at improving habitat suitability for grassland birds. We also reported few negative effects on other management priority species, making tree-removal a viable and defensible method for improving grassland quality. Our results to indicate that tree-removal, when conducted using common management techniques, may require multiple years before benefits are observed.

Table 1. Summary of treatments applied from 2005 to 2011 on fourteen grassland study sites in western Minnesota, USA. Codes are: B = burn, C = tree and shrub cutting, H = Haying, S = Spraying herbicide, and "--" indicates no treatment was applied. The subscripts for burn treatments indicate that one half, one third, or the entire site (all) was burned in that year. Tree- removal treatment took place in the fall and winter of 2005 and 2006 on treated (trt) sites (vertical dashed line) and NAs indicate site-year combinations that were omitted or where no surveys were conducted.

Site name	Group	2005	2006	2007	2008	2009	2010	2011
Arctander	Control	--	--	--	--	--	--	--
F. Slough	Control	--	--	--	$B_{1/2}$	$B_{1/2}$	--	--
Swan Lk.	Control	--	--	--	--	--	--	--
Hagstrom	Control	--	--	--	--	--	--	--
L. Slough	Control	--	--	--	--	NA	NA	NA
N. East	Control	--	--	--	--	NA	NA	NA
R. Forks	Control	NA	NA	--	--	--	--	--
Steger	Control	NA	NA	--	--	--	--	--
N. West	Trt	--	S	$B_{1/2}$, S	$B_{1/2}$, C	--	--	--
Thomson	Trt	--	--	$B_{1/2}$, S, C	$B_{1/2}$	--	--	--
Wente	Trt	--	$B_{1/2}$	$B_{1/2}$, C	--	--	H	--
B. Lake	Trt	B_{all}	--	$B_{1/2}$	$B_{1/2}$	--	--	C
Randall	Trt	--	$B_{1/2}$	--	$B_{1/2}$	--	--	$B_{1/2}$
Weber	Trt	--	--	$B_{1/3}$	$B_{1/3}$	$B_{1/3}$	--	--

Table 2. Abbreviations and description for 5 models that explain various responses to tree-removal treatment. All models included an intercept and random intercept term for site (n = 14). Models were used to test response of birds and vegetation to tree-removal treatment. Data based on point counts and vegetation surveys conducted from 2005-2011 in western Minnesota, USA. Tree removal treatments took place on 6 of 14 grassland sites in the winter of 2005-2006.

Model name	Model description
null	Null
yr-only	Annual variation, no treatment effect
trt.i-only$_a$	Treatment effect occurred in year 1 and was sustained throughout study, with little annual fluctuation in abundance
trt.i$_a$ + yr	Treatment effect occurred in year 1 and abundance varied annually, but was consistent between control and treatment sites after treatment
trt$_b$ × yr	Treatment effect occurred and interacted with annual effects; response to treatment varied annually

a = trt.i is an indicator representing if the treatment had taken place; control sites coded 0, treatment sites 1, and treatment sites before treatment are 0.

b = treatment an indicator based on if the site was control (= 0) or treated (= 1).

Table 3. Model comparisons (ΔAIC) for 16 individual species and 8 groups of species. All models included an intercept and a random site effect on the intercept (n = 14 sites). See table 2 for detailed description of models. Results are based on 1,756 point counts conducted from 2005-2011 in western Minnesota, USA. Tree removal treatments took place on 6 of 14 grassland sites in the winter of 2005-2006. Bold, underlined terms highlight the best approximating model and underlined numbers highlight competitive models (within 2 AIC of best model). Details on group composition can be found in Table 4.

Species or group	n	Null k = 2	Yr-only k = 8	Trt.i K = 3	Trt.i + yr k = 9	$Trt_b \times$ yr k = 15
Species modeled individually						
Spinus tristis	513	57.5	9.8	59.0	11.2	**<u>0.0</u>**
Molothrus ater	506	8.5	15.6	9.5	16.7	**<u>0.0</u>**
Dolichonyx oryzivorus	708	58.4	26.0	59.9	27.4	**<u>0.0</u>**
Spizella pallida	1332	30.4	20.4	31.9	22.0	**<u>0.0</u>**
Quiscalus quiscula	976	27.7	24.8	29.1	26.1	**<u>0.0</u>**
Geothlypis trichas	1688	12.8	**<u>0.0</u>**	14.6	<u>1.9</u>	8.4
Tyrannus tyrannus	394	6.5	4.0	7.4	5.0	**<u>0.0</u>**
Cistothorus palustris	592	6.2	**<u>0.0</u>**	7.7	<u>1.5</u>	2.2
Agelaius phoeniceus	3996	45.4	4.0	46.6	5.2	**<u>0.0</u>**
Cistothorus platensis	589	185.6	46.6	187.6	48.6	**<u>0.0</u>**
Melospiza melodia	1173	**<u>0.0</u>**	3.3	<u>2.0</u>	5.3	12.4
Melospiza Georgiana	554	16.4	**<u>0.0</u>**	18.4	<u>2.0</u>	10.0
Tachycineta bicolor	722	37.5	**<u>0.0</u>**	38.3	<u>0.7</u>	7.4
Empidonax traillii	199	**<u>0.0</u>**	<u>1.4</u>	<u>1.6</u>	3.0	6.9
Xanthocephalus xanthocephalus	454	86.0	3.9	87.6	5.5	**<u>0.0</u>**
Setophaga petechia	1110	21.3	14.5	23.3	16.5	**<u>0.0</u>**
Species modeled in groups						
All grassland birds	2733	160.6	73.2	149.8	75.0	**<u>0.0</u>**
General, tree/shrub-nest	678	10.6	13.3	**<u>0.0</u>**	9.3	9.0
Grassland ground-nest*	97	11.6	<u>2.0</u>	13.3	**<u>0.0</u>**	5.6

Waterfowl	715	78.2	44.8	53.6	27.4	**0.0**
Wetland, floating nest	212	3.5	11.2	4.5	9.2	**0.0**
Wetland, ground-nest	542	67.9	20.6	46.1	13.4	**0.0**
Woodland, Cavity-nest	275	55.6	44.9	1.6	**0.0**	6.1
Woodland, tree/shrub nest	812	63.9	32.7	**0.0**	2.6	2.6
Measures of vegetation response						
Average distance to tree	--	891.5	400.8	863.5	372.5	**0.0**
Average distance to shrub	--	116.3	59.0	111.0	53.7	**0.0**
Average distance to slash	--	945.7	388.1	920.5	362.6	**0.0**
Average litter depth	--	447.2	104.2	444.7	100.0	**0.0**
Average grass height/density	--	47.7	6.6	49.4	8.3	**0.0**

* = grassland ground-nest excludes species modeled individually, ground-nesting birds of prey, and invasive species.

a = treatment as indicator with control = 0, treatment = 1, treatment sites pre-treatment = 0

b = treatment an indicator based on if the site was in the control (= 0) or treated (= 1) group

Table 4. Summary of birds counted in 1,756 point counts during 2005-2011 in west-central Minnesota. Stars indicate species that are listed on Minnesota's list of conservation concern. The first 16 species were analyzed individually, the following 65 were combined into groups based on their nest-site and habitat preferences and the final 32 species were omitted from habitat groups. Waterfowl (Anseriformes) and an inclusive set of grassland birds (underlined) were also considered as groups, due to management priority status.

Species name	Scientific name	Total	Family	Nest site[a] - Habitat type[b]
species modeled individually				
Red-winged Blackbird	*Agelaius phoeniceus*	3996	Passeriformes	EV-wetland
Common Yellowthroat	*Geothlypis trichas*	1688	Passeriformes	WV-general
<u>Clay-colored Sparrow</u>	<u>*Spizella pallida*</u>	<u>1332</u>	<u>Passeriformes</u>	<u>WV-grassland/open</u>
Song Sparrow	*Melospiza melodia*	1173	Passeriformes	GR -general
Yellow warbler	*Setophaga petechia*	1110	Passeriformes	WV-general
Common Grackle	*Quiscalus quiscula*	976	Passeriformes	WV-trees
Tree Swallow	*Tachycineta bicolor*	722	Passeriformes	CV-trees/wetland
<u>Bobolink*</u>	<u>*Dolichonyx oryzivorus*</u>	<u>708</u>	<u>Passeriformes</u>	<u>GR -grassland</u>
Marsh Wren*	*Cistothorus palustris*	592	Passeriformes	EV-wetland
<u>Sedge Wren*</u>	<u>*Cistothorus platensis*</u>	<u>589</u>	<u>Passeriformes</u>	<u>GR –wet/grassland</u>
Swamp Sparrow*	*Melospiza georgiana*	554	Passeriformes	EV-wetland
American Goldfinch	*Spinus tristis*	513	Passeriformes	WV-general
Brown-headed Cowbird	*Molothrus ater*	506	Passeriformes	NA-general
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	454	Passeriformes	EV-wetland
Eastern Kingbird	*Tyrannus tyrannus*	394	Passeriformes	WV-general
Willow Flycatcher*	*Empidonax traillii*	199	Passeriformes	WV-trees/wetland
Groups, based on nest site and habitat preferences				

House Wren	*Troglodytes aedon*	120	Passeriformes	CV-trees
Black-capped Chickadee	*Poecile atricapillus*	42	Passeriformes	CV-trees
Great Crested Flycatcher	*Myiarchus crinitus*	34	Passeriformes	CV-trees
Northern Flicker	*Colaptes auratus*	31	Piciformes	CV-trees
White-breasted Nuthatch	*Sitta carolinensis*	22	Passeriformes	CV-trees
Downy Woodpecker	*Picoides pubescens*	20	Piciformes	CV-trees
Hairy Woodpecker	*Picoides villosus*	2	Piciformes	CV-trees
Red-bellied Woodpecker	*Melanerpes carolinus*	2	Piciformes	CV-trees
Pileated Woodpecker	*Dryocopus pileatus*	1	Piciformes	CV-trees
Yellow-bellied Sapsucker*	*Sphyrapicus varius*	1	Piciformes	CV-trees
Black Tern*	*Chlidonias niger*	81	Charadriiformes	FL-wet
Pied-billed Grebe	*Podilymbus podiceps*	53	Podicipediformes	FL-wet
Sora	*Porzana carolina*	25	Gruiformes	FL-wet
American Coot	*Fulica americana*	22	Gruiformes	FL-wet
Redhead	*Aythya americana*	12	Anseriformes	FL-wet
Canvasback	*Aythya valisineria*	9	Anseriformes	FL-wet
Red-necked Grebe*	*Podiceps grisegena*	8	Podicipediformes	FL-wet
Eared Grebe*	*Podiceps nigricollis*	1	Podicipediformes	FL-wet
Forster's Tern*	*Sterna forsteri*	1	Charadriiformes	FL-wet
Horned Lark	*Eremophila alpestris*	3	Passeriformes	GR -grassland
Savannah Sparrow	*Passerculus sandwichensis*	39	Passeriformes	GR -grassland
Grasshopper Sparrow*	*Ammodramus savannarum*	16	Passeriformes	GR -grassland
Vesper Sparrow	*Pooecetes gramineus*	13	Passeriformes	GR -grassland
Western Meadowlark	*Sturnella neglecta*	12	Passeriformes	GR -grassland

Upland Sandpiper*	*Bartramia longicauda*	9	Charadriiformes	GR -grassland
Le Conte's Sparrow*	*Ammodramus leconteii*	5	Passeriformes	GR -grassland
Canada Goose	*Branta canadensis*	47	Anseriformes	GR -wet
Ruddy Duck	*Oxyura jamaicensis*	21	Anseriformes	GR -wet
Ring-necked Duck	*Aythya collaris*	8	Anseriformes	GR -wet
Virginia Rail*	*Rallus limicola*	4	Gruiformes	GR -wet
American Bittern*	*Botaurus lentiginosus*	3	Pelicaniformes	GR -wet
Wilson's Snipe	*Gallinago delicata*	3	Charadriiformes	GR -wet
Least Bittern	*Ixobrychus exilis*	2	Pelicaniformes	GR -wet
Mallard	*Anas platyrhynchos*	232	Anseriformes	GR –wet/grassland
Blue-winged Teal	*Anas discors*	211	Anseriformes	GR –wet/grassland
Gadwall	*Anas strepera*	9	Anseriformes	GR –wet/grassland
Northern Shoveler	*Anas clypeata*	2	Anseriformes	GR –wet/grassland
Gray Catbird	*Dumetella carolinensis*	243	Passeriformes	WV-general
Mourning Dove	*Zenaida macroura*	241	Columbiformes	WV-general
American Robin	*Turdus migratorius*	124	Passeriformes	WV-general
Brown Thrasher*	*Toxostoma rufum*	43	Passeriformes	WV-general
Brewer's Blackbird	*Euphagus cyanocephalus*	19	Passeriformes	WV-general
Chipping Sparrow	*Spizella passerina*	7	Passeriformes	WV-general
House Finch	*Carpodacus mexicanus*	4	Passeriformes	WV-general
Western Kingbird	*Tyrannus verticalis*	4	Passeriformes	WV-general
Orchard Oriole	*Icterus spurius*	190	Passeriformes	WV-trees
Warbling Vireo	*Vireo gilvus*	150	Passeriformes	WV-trees
Least Flycatcher*	*Empidonax minimus*	91	Passeriformes	WV-trees
Cedar Waxwing	*Bombycilla cedrorum*	88	Passeriformes	WV-trees
Baltimore Oriole	*Icterus galbula*	75	Passeriformes	WV-trees
Rose-breasted Grosbeak*	*Pheucticus ludovicianus*	52	Passeriformes	WV-trees
Red-eyed Vireo	*Vireo olivaceus*	38	Passeriformes	WV-trees

Black-billed Cuckoo	*Coccyzus erythropthalmus*	23	Cuculiformes	WV-trees
Blue Jay	*Cyanocitta cristata*	16	Passeriformes	WV-trees
Eastern Wood-Pewee*	*Contopus virens*	15	Passeriformes	WV-trees
Indigo Bunting	*Passerina cyanea*	15	Passeriformes	WV-trees
Yellow-throated Vireo	*Vireo flavifrons*	14	Passeriformes	WV-trees
American Redstart	*Setophaga ruticilla*	13	Passeriformes	WV-trees
Olive-sided Flycatcher*	*Contopus cooperi*	9	Passeriformes	WV-trees
American Crow	*Corvus brachyrhynchos*	8	Passeriformes	WV-trees
Ruby-throated Hummingbird	*Archilochus colubris*	5	Apodiformes	WV-trees
Scarlet Tanager	*Piranga olivacea*	4	Passeriformes	WV-trees
Yellow-billed Cuckoo	*Coccyzus americanus*	3	Cuculiformes	WV-trees
Northern Cardinal	*Cardinalis cardinalis*	2	Passeriformes	WV-trees
Eastern Phoebe	*Sayornis phoebe*	1	Passeriformes	WV-trees
Omitted from nest-site/habitat groups				
Cooper's Hawk	*Accipiter cooperii*	8	Accipitriformes	omit
Red-tailed Hawk	*Buteo jamaicensis*	6	Accipitriformes	omit
Great Horned Owl	*Bubo virginianus*	3	Strigiformes	omit
Green Heron	*Butorides virescens*	16	Pelecaniformes	omit
Great Egret	*Ardea alba*	59	Pelecaniformes	omit
Great Blue Heron	*Ardea herodias*	16	Pelecaniformes	omit
Black-crowned Night-Heron*	*Nycticorax nycticorax*	3	Pelecaniformes	omit
Wood Duck	*Aix sponsa*	146	Anseriformes	omit
European Starling	*Sturnus vulgaris*	7	Passeriformes	omit
Hooded Merganser	*Lophodytes cucullatus*	18	Anseriformes	omit
American Kestrel	*Falco sparverius*	1	Accipitriformes	omit

Ring-necked Pheasant	*Phasianus colchicus*	129	Galliformes	omit
Killdeer	*Charadrius vociferus*	31	Charadriiformes	omit
Field Sparrow*	*Spizella pusilla*	35	Passeriformes	omit
Common Loon*	*Gavia immer*	2	Gaviiformes	omit
White-crowned Sparrow	*Zonotrichia leucophrys*	1	Passeriformes	omit
Ring-billed Gull	*Larus delawarensis*	14	Charadriiformes	omit
Veery*	*Catharus fuscescens*	8	Passeriformes	omit
Ovenbird*	*Seiurus aurocapilla*	4	Passeriformes	omit
Tree Sparrow	*Oceanodroma tristrami*	2	Passeriformes	omit
Wild Turkey	*Meleagris gallopavo*	1	Galliformes	omit
Barn Swallow	*Hirundo rustica*	94	Passeriformes	omit
Purple Martin	*Progne subis*	47	Passeriformes	omit
Cliff Swallow	*Petrochelidon pyrrhonota*	21	Passeriformes	omit
Turkey Vulture	*Cathartes aura*	2	Accipitriformes	omit
American White Pelican*	*Pelecanus erythrorhynchos*	107	Pelecaniformes	omit
Double-crested Cormorant	*Phalacrocorax auritus*	21	Suliformes	omit
Eastern Bluebird	*Sialia sialis*	9	Passeriformes	omit
Belted Kingfisher	*Megaceryle alcyon*	3	Coraciiformes	omit
Chimney Swift	*Chaetura pelagica*	1	Apodiformes	omit
Spotted Sandpiper	*Actitis macularius*	1	Charadriiformes	omit
Northern Harrier*	*Circus cyaneus*	7	Accipitriformes	omit

a. Nest site codes: EV = emergent vegetation in wetlands; CV = nest in tree cavity; GR = nest directly on ground or in low, non-woody vegetation; FL= floating nest; WV = nest located in woody vegetation (trees or shrubs)

b. Habitat codes: wet = water, wetlands, marshes, sedges, wet meadows; general = edges, scrub, shrubland, scattered trees in open land; grassland = grassland; Trees= generally woody habitat like forest, parkland, thickets

* indicates species of conservation concern in the state of Minnesota (Minnesota Department of Natural Resources)

Table 5. Model estimates of coefficients and standard errors for interaction terms for species and groups where the best-approximating model was trt × yr. All significant terms are in bold, significant positive terms are underlined. All estimates are from generalized linear mixed models with a random intercept of site (n = 14) and Poisson error structure. See table 4 for scientific names and composition of species groups.

Species/group	$Year_1$×Trt	$Year_2$×Trt	$Year_3$×Trt	$Year_4$×Trt	$Year_5$×Trt	$Year_6$×Trt
American Goldfinch	**-0.86 (0.32)**	-0.16 (0.31)	**-1.01 (0.38)**	**-1.43 (0.46)**	**-1.04 (0.31)**	**-0.73 (0.31)**
Brown-headed Cowbird	-0.02 (0.38)	-0.32 (0.35)	-0.66 (0.36)	**-1.56 (0.37)**	**-1.16 (0.37)**	**-0.76 (0.37)**
Bobolink	0.17 (0.25)	**-1.35 (0.33)**	0.19 (0.26)	0.36 (0.27)	0.09 (0.31)	0.43 (0.3)
Clay-colored Sparrow	0.02 (0.2)	-0.34 (0.21)	**-0.54 (0.21)**	0.21 (0.21)	0.11 (0.2)	**0.64 (0.23)**
Common Grackle	-0.17 (0.25)	0.12 (0.24)	**-0.95 (0.26)**	**-1.08 (0.27)**	-0.29 (0.24)	-0.43 (0.24)
Eastern Kingbird	0.12 (0.35)	0.08 (0.35)	**-0.93 (0.41)**	-0.37 (0.41)	-0.45 (0.4)	0.65 (0.41)
Red-winged Blackbird	-0.11 (0.12)	0.2 (0.12)	-0.16 (0.12)	-0.03 (0.12)	0.05 (0.12)	-0.22 (0.12)
Sedge Wren	-0.15 (0.3)	**-1.45 (0.36)**	-0.12 (0.34)	0.41 (0.27)	**1.01 (0.31)**	0.41 (0.57)
Yellow-headed Blackbird	**0.78 (0.37)**	**0.86 (0.29)**	0.52 (0.35)	0.04 (0.35)	**0.96 (0.44)**	**1.12 (0.46)**
Yellow Warbler	-0.12 (0.22)	-0.38 (0.22)	**-0.9 (0.23)**	**-0.77 (0.23)**	**-0.8 (0.23)**	**-0.75 (0.22)**
All grassland birds	0.06 (0.14)	**-0.69 (0.15)**	-0.19 (0.14)	**0.32 (0.14)**	**0.39 (0.14)**	**0.61 (0.16)**
Waterfowl	**0.70 (0.34)**	**1.76 (0.36)**	**0.70 (0.34)**	**1.20 (0.37)**	**1.62 (0.36)**	**1.82 (0.34**
Wetland- floating nest	0.74 (0.52)	1.00 (0.54)	**1.81 (0.53)**	-0.62 (0.68)	**1.36 (0.53)**	1.02 (0.57)
Wetland- ground nest	0.58 (0.43)	**1.68 (0.44)**	**1.02 (0.43)**	**1.02 (0.46)**	**1.73 (0.48)**	**1.63 (0.43)**

Figure 1. Location of 14 study sites in west-central Minnesota, USA. The study began in 2005 with 12 grassland sites, 6 control (black circles) and 6 pending extensive tree-removal treatment (black stars) during the winter of 2005-2006. Two additional control sites were added in 2007 (grey circles), and two original control sites were eventually treated in 2008 (grey stars) and subsequently dropped from our analysis.

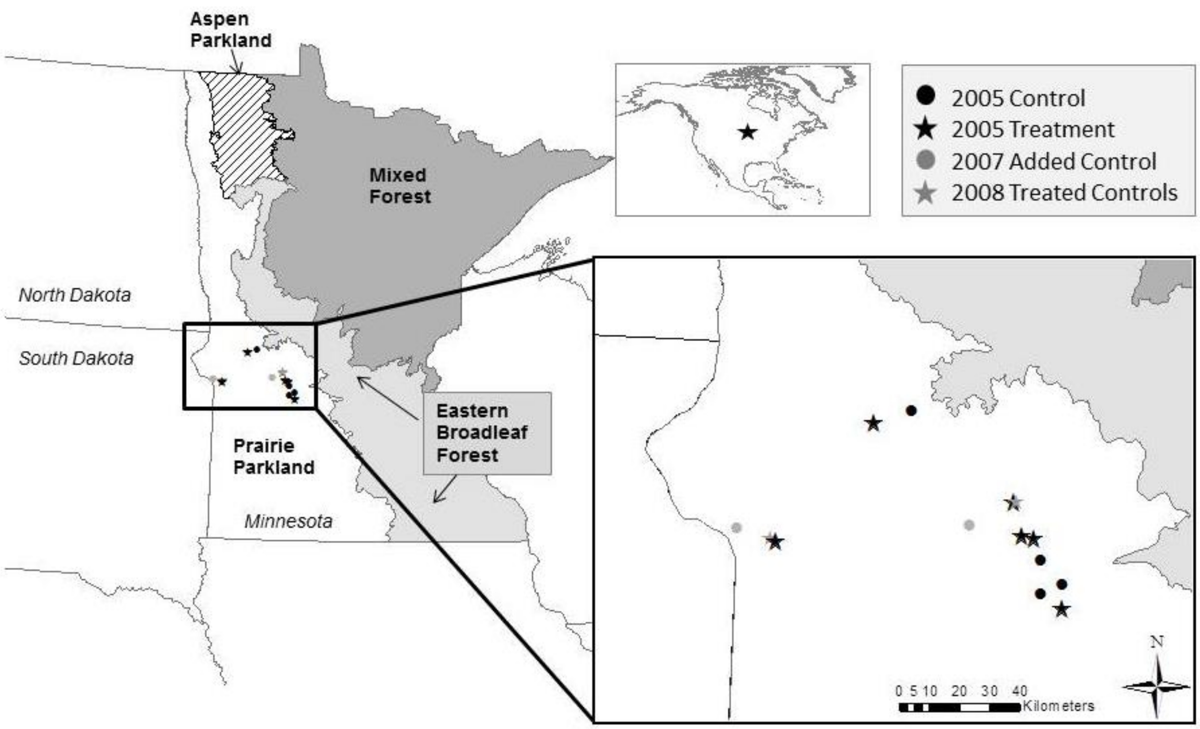


Figure 2. Hypothetical responses to tree-removal treatment include transient, immediate, delayed and no effect. Note that all potential responses could also occur in the negative direction and that we expect any real measurement to have annual fluctuations.

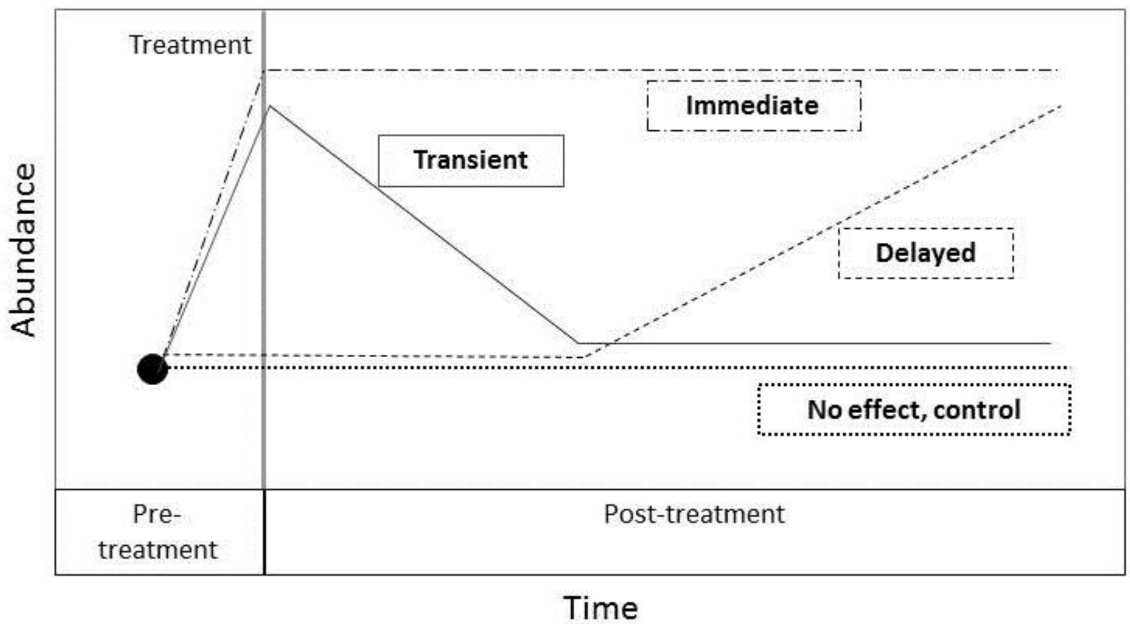


Figure 3. Model-based estimates and 95% prediction intervals of vegetation response to experimental tree-removal. Measurements were taken before (year 2005 or year 0) and after (years 2006-2011 or 1-6) tree-removal at 6 treatment and 8 control sites in west-central Minnesota. Average distance to tree, shrub, and slash measurements represent the mean distance to a feature (from 4 cardinal directions) with a maximum of 600, 200, or 800 (respectively) when no tree, shrub, or slash existed in a quadrant. Minus and plus signs denote significant negative or positive treatment effects, respectively ($p < 0.05$).

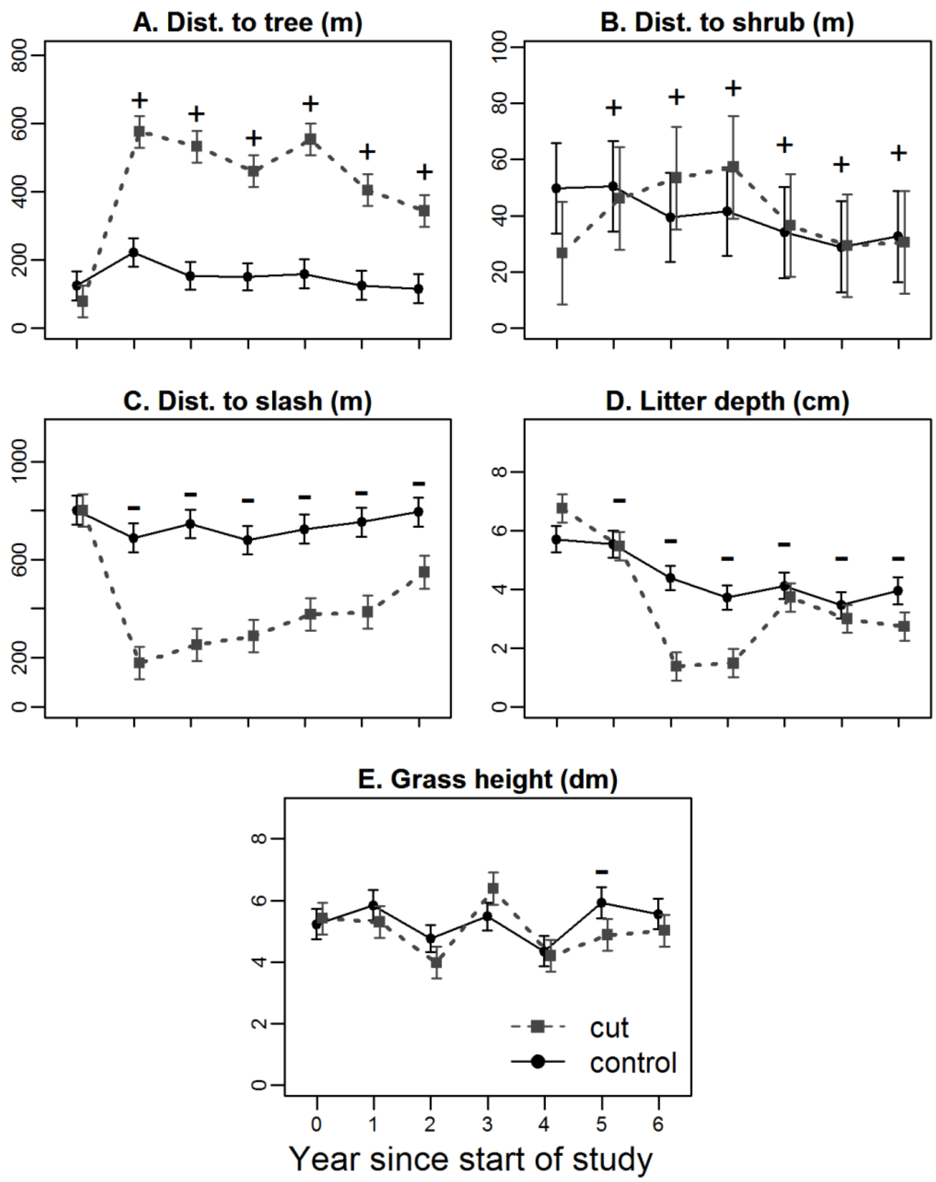
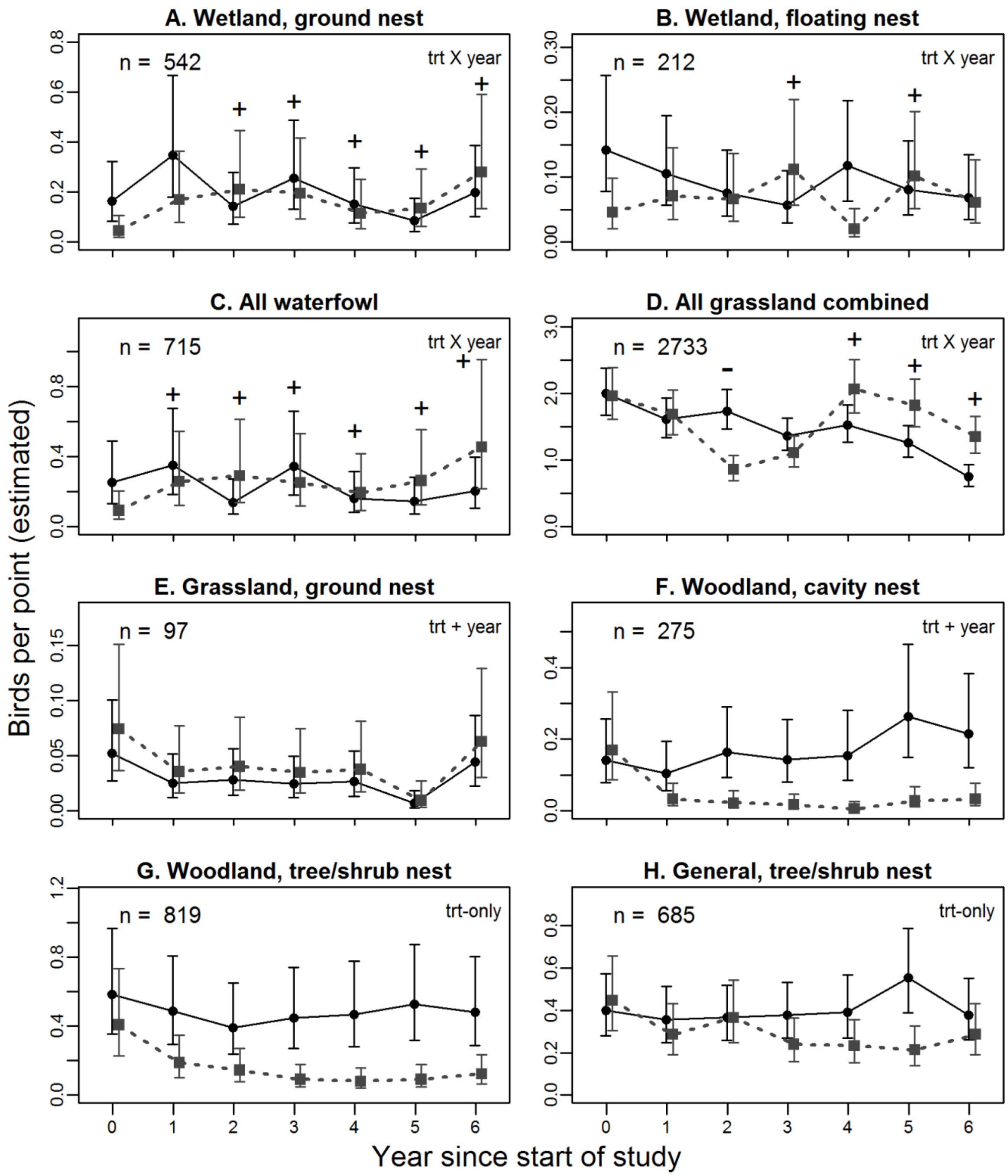
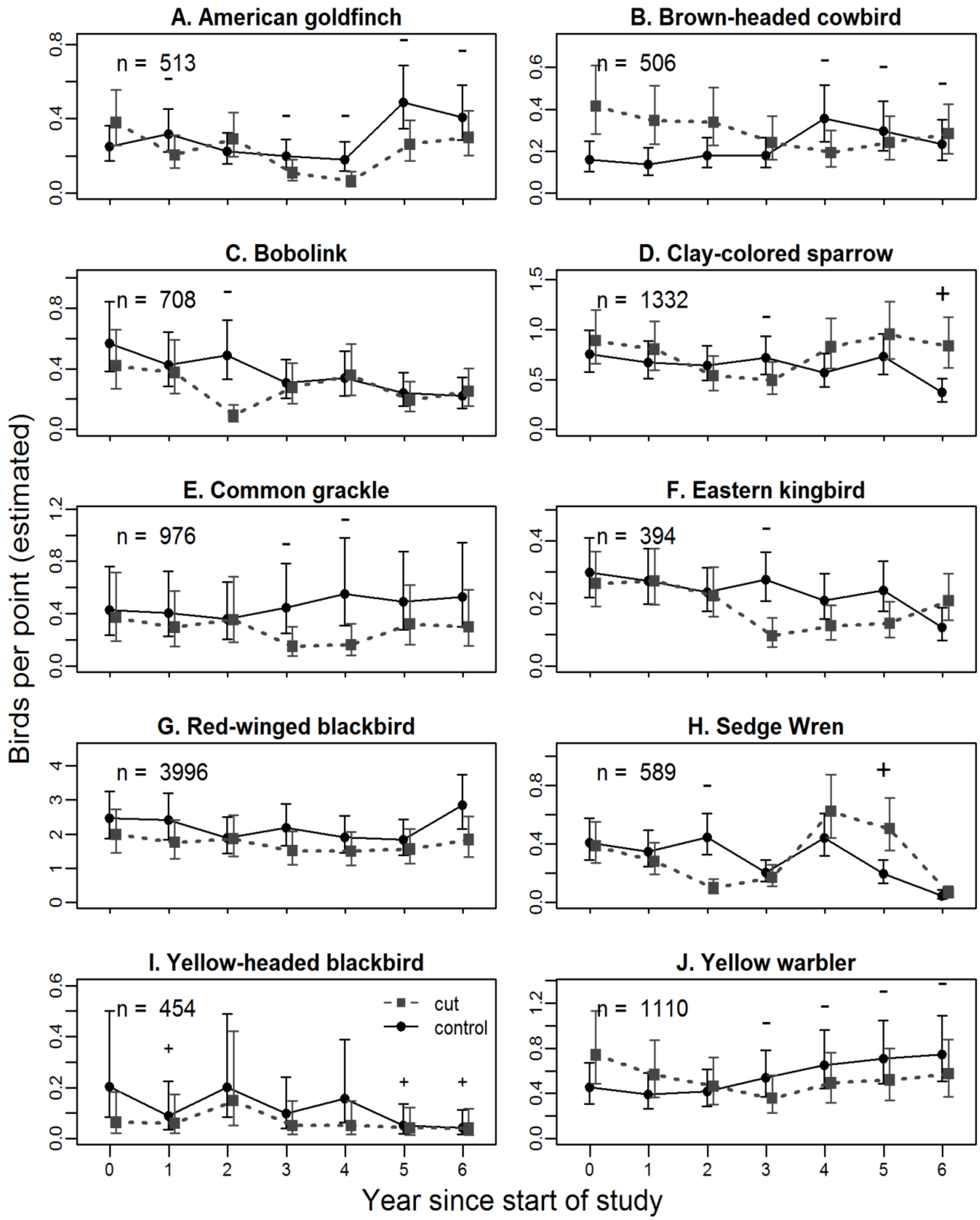


Figure 4. Model-based estimates of average bird count (with 95% prediction interval) per point on sites where extensive tree-removal treatment took place (grey, dashed) and control sites (black, solid). The composition of the groups was determined by preferred nest and foraging sites (see Table 4 for details), as well as two groups of management priority (waterfowl, all grassland birds combined). Results are based on data from 1,756 point counts conducted at 14 sites over 7 years in west-central Minnesota, USA. Minus and plus-signs denote significant negative or positive effect of treatment in that year ($p > 0.05$). Plots for all groups are based on trt × year model, but the best-approximating model for the group is noted in upper right of plot.



A. Wetland, ground nest
n = 542
trt X year
B. Wetland, floating nest
n = 212
trt X year
C. All waterfowl
n = 715
trt X year
D. All grassland combined
n = 2733
trt X year
E. Grassland, ground nest
n = 97
trt + year
F. Woodland, cavity nest
n = 275
trt + year
G. Woodland, tree/shrub nest
n = 819
trt-only
H. General, tree/shrub nest
n = 685
trt-only
Birds per point (estimated)
Year since start of study

Figure 5. Model-based estimates of mean and 95% prediction intervals for focal species; control sites (black, solid) and on sites that underwent tree-removal treatment (grey, dashed) in the winter between study year 0 and 1. Results are based on 1,756 point counts conducted during 2005-2011 in west-central Minnesota. Minus-signs denote a significant, negative effect of treatment ($p > 0.05$) and plus-sings denote significant, positive treatment effects.


A. American goldfinch
n = 513
B. Brown-headed cowbird
n = 506
C. Bobolink
n = 708
D. Clay-colored sparrow
n = 1332
E. Common grackle
n = 976
F. Eastern kingbird
n = 394
G. Red-winged blackbird
n = 3996
H. Sedge Wren
n = 589
I. Yellow-headed blackbird
n = 454
cut
control
J. Yellow warbler
n = 1110
Birds per point (estimated)
Year since start of study

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